THE UNIVERSITY OF ALBERTA

CONTRIBUTION TO THE TAXONOMY OF *OXYTROPIS CAMPESTRIS* (L.) DC. IN NORTHWESTERN NORTH AMERICA

by

© WAYNE J. ELISENS

A THESIS

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled Contribution to the Taxonomy of *Oxytropis campestris* (L.) DC. in Northwestern North America

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ABSTRACT

The *Oxytropis campestris* complex in northwestern North America is a polyploid series comprised of at least seven morphologically and geographically distinct taxa. In light of the data of the present study, the author proposes that five taxa be reelevated to species status (*O. cusickii* Greenm., *O. gracilis* (A. Nels.) K. Schum., *O. columbiana* St. John, *O. jordalii* Porsild, *O. varians* (Rydb.) K. Schum.) and that two taxa be recombined as subspecies: *O. gracilis* (A. Nels.) K. Schum. subsp. *dispar* (A. Nels.) Elisens and *O. jordalii* Porsild subsp. *davisii* (Welsh) Elisens.

Three different chromosome numbers are present in the complex and represent the tetraploid (2n=32), hexaploid (2n=48), and dodecaploid (2n=96) condition. Although three species have uniform chromosome numbers (*O. cusickii*, 2n=48; *O. jordalii*, 2n=32; and *O. columbiana*, 2n=48), two taxa, *O. varians* and *O. gracilis* subsp. *gracilis*, each exhibit two different chromosome numbers. No attempt to subdivide *O. varians* was undertaken since, with the exception of guard cell size, no differences were observed between hexaploid and dodecaploid representatives. At least two distinct entities may be present in *O. gracilis* subsp. *gracilis*. Although morphologically, cytologically (2n=32), and ecologically uniform

east of the continental divide, subsp. *gracilis* is quite variable in appearance and has a different chromosome number (2n=48) west of the divide.

The chemical data indicate that of the thirty-three different flavonoid glycosides characterized, the majority were restricted in their occurrence. Only eleven glycosides were present in two or more taxa reinforcing the morphological, cytological, and geographical distinctiveness of the taxa examined in the present study.

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CHAPTER 1.

INTRODUCTION

The genus *Oxytropis* DC. is one of about 600 genera that comprise the Leguminosae, the third largest Angiosperm family. Second only to the grasses in economic importance, legumes provide many articles of food, fodder, dyes, gums, resins, oils, and ornament. The family is cosmopolitan in its distribution and is usually divided into three subfamilies: the Mimosoideae, the Caesalpinoideae, and the Lotoideae (Bentham, 1865; Taubert, 1894). These three taxa can be distinguished as follows:

Mimosoideae: flowers actinomorphic, calyx and corolla valvate in the bud.

Caesalpinoideae: flowers weakly or strongly zygomorphic, caesalpinaceous (upper petal innermost), aestivation imbricate-ascending.

Lotoideae: flowers strongly zygomorphic, papilionaceous (upper petal outermost), aestivation imbricate-descending, the two anterior petals often basally connate (the keel).

These taxa have, however, been accorded various taxonomic treatments; they have been classified by various authors as distinct families (Hutchinson, 1926; Taktahjan, 1959), reduced to two families (Wettstein, 1933), or

expanded to four subfamilies (DeCandolle, 1802). As Heywood (1971) notes, there is still no general agreement regarding the treatment of the major divisions.

The inclusion of *Oxytropis* in the tribe Galegeae (subfamily Lotoideae) has, to the contrary, rarely been disputed since Bentham's account of the Leguminosae in 1865. The second largest tribe in the legumes, the Galegeae is comprised of about fifty-four genera. Its members are primarily temperate in distribution and possess pinnately compound leaves with entire leaflets as well as ten stamens (usually diadelphous) with equal anthers. *Oxytropis*, with about 300 species worldwide, is one of the largest genera in the tribe. Best represented in Europe and Asia, there are only 20-30 species of *Oxytropis* currently recognized in North America (Barneby, 1952).

DeCandolle, working exclusively with Old World material, erected the genus *Oxytropis* in 1802 to contain a part of the Linnean *Astragalus*. As first described, *Oxytropis* was characterized by the beaked keel petals and the introflexion of the pod's ventral suture, as opposed to the muticous keel and bilocular pod (from the dorsal suture) of *Astragalus*. Since DeCandolle's treatise, certain authors have continued to combine the two genera (for example, Tidestrom, 1937; Shinners, 1958). Systematists in favor of reducing *Oxytropis* to subgeneric rank point to the lack of a distinctive habit and of any abso-

lute criteria by which the two genera can be set apart. Indeed, the description of two perfect astragali, *Astragalus nothoxys* Gray and *Astragalus acutrostis* Wats., with distinctly cuspidate keels resulted in several authors (for example, Rouy, 1897) removing the species of *Oxytropis* into a subgenus of *Astragalus*. However, Bunge (1869), the monographer of Old World *Astragalus* and of *Oxytropis*, Taubert (in Engler's Pflanzenfamilien, 1894), as well as Bentham and Hooker, and most contemporary botanists, have supported DeCandolle's treatment (see Wheeler, 1939). Barneby (1952), in his revision of the genus in North America, stated that until it could be shown that the gap between the two genera is no greater than that existing between sections within *Astragalus*, or that there are species of *Oxytropis* referable with equal justice to either genus, or that *Oxytropis* is polyphyletic, the submergence of *Oxytropis* in the older genus would do nothing to clarify relationships.

Chromosome data support the claim that *Oxytropis* presents a unified phyletic group related to, but distinct from, the *Astragalus* assemblage. The basic chromosome number in *Oxytropis* is consistently X=8, whereas *Astragalus* has basic numbers of 8 (Old World species) and 11, 12, or 13 in the New World (Ledingham and Fahselt, 1967).

OXYTROPIS DC.[1]

Oxytropis DC. Astragal. 24:77, 1802. *nom. cons.*

Aragallus Neck. Elem. 3:12, 1790.

Spiesia Neck. Elem. 3:13, 1790.

Astragalus L. Sp. Pl. 755, 1753. *pro parte.*

> Plants perennial, herbaceous, acaulescent to short caulescent; leaves alternate or basal, odd-pinnate, leaflets entire, without stipels; stipules mostly connate, adnate to the petiole or free; flowers violet, purple, white or yellow, in axillary racemes or spikes or arising from the caudex; bracts often small, membranous; bracteoles minute or absent; calyx-tube cylindric to campanulate, five subequal teeth; petals often with rather long claws; banner erect, ovate or oblong; keel equal to the wings or shorter, keel-tip produced into a beak, maculate or immaculate; wings oblong; stamens diadelphous, anthers uniform, ovary sessile or stipitate; style filiform straight or curved; pod sessile to stipitate, straight, erect or reflexed, two-loculed through intrusion of ventral suture to one-loculed; several seeded; seeds reniform, funicle filiform.

The first synopsis of the North American species of *Oxytropis* was by W.J. Hooker (1834) in his Flora Boreali-Americana. Although several species were first described in this important work (for example, *O. splendens*), the paucity of the material available limited Hooker's account of the genus as it did that of Torrey and Gray in their Flora of North America (1838). A similar problem faced Bunge (1869) in his monograph of *Oxytropis*. Asa Gray (based on his extensive collections and examination

[1] synonymy based on Welsh (1967)

of the material at Kew) published the first North American revision (1884). He recognized sixteen species. The onset of the twentieth century witnessed further activity not only in the field, but in the proliferation of species proposed by various workers. Many of these species were hastily proposed, often based on one or two specimens, and, in Barneby's (1952) words, often contributed "... more to the literature and synonymy than to a true understanding of the genus."

In addition to the proliferation of newly described species, the resurrection of *Aragallus* Neck. and *Spiesia* Neck. by several authors, as well as the shifting back and forth between *Astragalus* and *Oxytropis*, resulted in chaos on the shelves of many herbaria. It was that disorder which prompted Barneby (1952) to attempt the first revision of the North American species of *Oxytropis* since Gray (1884). Barneby recognized twenty-two species; his account contributed greatly towards a definition of the major forms and a stabilization of the nomenclature. More recently, workers in the genus have generally supported Barneby's species concepts and have simply addended his original characterizations (for example, Boivin, 1967; Welsh, 1960, 1963, 1967).

Biosystematic studies within *Oxytropis* have been confined primarily to reports of chromosome numbers. As mentioned previously, the works of Ledingham and Fahselt

(1967) and Senn (1937) have consistently indicated that the basic number in the genus is X=8. These and other studies (for example, Ledingham, 1960; Holmen, 1962; Zhukova, 1966) indicate that *Oxytropis* is comprised of a number of polyploid species. In North America, chromosome counts range from 2n=16 in *O. deflexa* and *O. podocarpa* through 2n=32 (*O. viscida*) and 2n=48 *O.* (*sericea*) to a high of 2n=96 in *O. maydelliana* (Ledingham, 1960; Holmen, 1962). Aneuploidy does not appear to occur in the genus.

Although few chemosystematic studies have been carried out in *Oxytropis*, a wide variety of flavonoids have been identified in the Leguminosae from the numerous surveys conducted at the tribal and generic levels (Harborne, 1967; Peckett, 1959). Representative compounds from practically every one of the numerous flavonoid classes occur in the legumes as well as several compounds with unusual structures (Torck, 1976). The Leguminosae are particularly rich in methylated flavonols and flavones, additional hydroxylation in the flavonoid nucleus, and absence of hydroxylation at position 5 (Harborne, 1971). For example, 6- and 8- hydroxylated flavonols, methyl ethers related to the common flavonols (for example, isorhamnetin), and flavonols with a 2' hydroxylation are known in the family.

In addition to the several flavonoid structures

characteristic of the Legumimosae, each subfamily tends to have certain characteristic flavonoids or related phenolics (Harborne, 1967). While the Mimosoideae are rich in catechins, leucoanthocyanidins, and other tannins; the Caesalpinoideae have ellagitannins and the rare heartwood pigments haematoxylon and brazilin. Isoflavones and rotenoids characterize the Lotoideae; this subfamily is also particularly rich in anthocyanins and flavonol glycosides.

The few flavonoid surveys of *Oxytropis* reported in the literature have been carried out by Soviet workers (Pakanaev *et al*, 1969; Dungerdorzh and Petrenko, 1973; Blinova, 1974). Only Dungerdorzh and Petrenko's work has resulted in the identification of a flavonoid glycoside (rutin); most studies have been concerned with determination of the aglycone moieties in several Eurasiatic species. It is significant that the common flavonols quercetin and kaempferol are present in the majority of the species surveyed while rhamnetin and myricetin are more limited in their occurrence (Pakanaev *et al*, 1969; Blinova, 1974). No flavone aglycones are noted by any of these workers.

The present investigation is concerned with *Oxytropis campestris* (L.)DC. *sensu lato* in northwestern North America. Originally described in Linneus' (1753) Species Plantarum, *O. campestris* has been characterized by its

chartaceous pod texture, relatively small size of the flowers (<18mm.), and the more than six flowers per raceme. As with many Linnean species, further botanical exploration and study have revealed that *O. campestris sensu* Linneus is extremely variable with respect to its morphological features. Differences in stature, number of leaflets, length and density of the raceme, as well as the number and colour of the flowers have been noted by various authors (Porsild, 1951; Barneby, 1952; Welsh, 1963).

In addition to this morphological diversity, the circumboreal constellation of forms referred to as *O. campestris* (L.)DC. occur in a variety of geographic regions that exhibit much topographical and ecological diversity. In northwestern North America, where *O. campestris* is particularly widespread, its range extends from the Dakotas and northern Colorado to Alaska, the Yukon, and the western regions of the Northwest Territories (Barneby, 1952; Welsh, 1967). Within this region, several morphological taxa are common in, and, indeed, restricted to prairie, alpine, boreal, and arctic habitats. *O. campestris* is, therefore, comprised of a number of morphologically distinctive allopatric forms (Maps 1 & 2).

Oxytropis campestris (L.)DC.

Oxytropis campestris (L.)DC., Astrag., 59, 1802.
Astragalus campestris L., Sp. Pl.761. 1753, *sensu ampliatissimo.*

Oxytropis lambertii Hook., Fl. Bor.-Amer., 1: 107. 1834.
Oxytropis monticola Gray, Proc. Amer. Acad., 20:6. 1884. *pro max. parte.*
Spiesia monticola (Gray) O. Kze., Rev. Gen., 206. 1891.
Aragallus monticola (Gray) Greene, Pittonia, 3:212. 1897.
Oxytropis cusickii Greenm., Erythea, 7:116. 1899.
Aragallus gracilis A.Nels., Erythea, 7:60. 1899.
Aragallus dispar A. Nels., Erythea, 7:61. 1899.
Aragallus alpicola Rydb., Mem. N.Y. Bot. Gard., 1:252. 1900.
Aragallus villosus Rydb., Bull. Torr. Club, 28:36. 1901.
Aragallus varians Rydb., Bull. N.Y. Bot. Gard., 2:176. 1901.
Oxytropis gracilis (A.Nels.) K. Schum., Just's Jahresb., 27:496. 1901.
Oxytropis dispar (A. Nels.) K. Schum., Just's Jahresb., 27:496. 1901.
Oxytropis villosa (Rydb.) K. Schum., Just's Jahresb., 29:543. 1903.
Oxytropis varians (Rydb.) K. Schum., Just's Jahresb., 29:543. 1903.
Aragallus luteolus Greene, Proc. Biol. Soc. Wash., 18:17. 1905.
Aragallus albertinus Greene, Proc. Biol. Soc. Wash., 18:15. 1905.
Aragallus cervinus Greene, Proc. Biol. Soc. Wash., 18:16. 1905.
Aragallus macounii Greene, l. c., *pro parte.*
Oxytropis alpicola (Rydb.) Jones, Mont. Bot. Notes, 37. 1910. *non* Turcz. (1842).
Oxytropis luteola (Greene) Piper & Beattie, Fl. N.W. Coast, 337. 1915.
Oxytropis alaskana A. Nels., Univ. Wyo. Pub. Bot., 1:120. 1926.
Oxytropis rydbergii A. Nels., Univ. Wyo. Pub. Bot., 1:117. 1926.
Oxytropis paysoniana A. Nels., Univ. Wyo. Pub. Bot., 1:119. 1926.
Oxytropis olympica St. John, Proc. Biol. Soc. Wash., 41:103. 1928.
Oxytropis mazama St. John, op. cit., 101. 1928.
Oxytropis okanoganea St. John, op. cit., 102. 1928.
Oxytropis cascadensis St. John, op. cit., 105. 1928.
Oxytropis columbiana St. John, op. cit., 100. 1928.
Oxytropis albertina (Greene) Rydb., Fl. Prair. & Pl., 484. 1932.
Astragalus rydbergianus Tidestr., Proc. Biol. Soc. Wash., 50:19. 1937. (*non. A. villosus*

Mchx).
Astragalus albertinus (Greene) Tidestr., Proc. Biol. Soc. Wash., 50:19. 1937.
Astragalus alpicola (Rydb.) Tidestr., Proc. Biol. Soc. Wash., 50:19. 1937.
Astragalus mazama (St. John) G.N. Jones, Univ. Wash. Pub. Bot., 7:175. 1938.
Astragalus grayanus Tidestr., in Tidestr. & Kitt., Gl. Ariz. & New Mex., 216. 1941. *quoad nom.* (*non A. monticola* Phil.).
Oxytropis hyperborea Porsild, Sargentia, 4:53. 1943.
Oxytropis jordalii Porsild, Canad. Field-Nat., 65:77. 1951.

Description of *Oxytropis campestris* (L.) DC.

Variable in stature and pubescence, green and glabrate to densely silky-pilose, sometimes villous-hirsute especially the scape and petiole; caespitose and acaulescent from a branching caudex; stipules membranous, pale, glabrous to pilose dorsally, triangular to lanceolate acuminate, connate, adnate to the petioles, 1-3 nerved, the margins naked or ciliate with bristles or clavate processes; leaves 5-25 cm. long; leaflets 7-45, scattered, opposite or sometimes geminate and verticellate, 9-25 mm. long, 3-8 mm. wide; scapes 2.5-36 cm. long; bracts narrowly lanceolate, longer than the pedicels, pilose dorsally, rarely glabrate; racemes 5-30 flowered, 3-24 cm. long, capitate to oblong, becoming lax, 0.5-11 cm. long in fruit; calyx cylindrical with dark and light hairs, the tube 4.5-7 mm. long, teeth 1-4 mm. long, triangular; corolla white, ochroleucous, pale yellow, pinkish or purplish; banner 12-20 mm. long, 4-8 mm. wide; wings 10-17 mm. long, blades not much dilated upward, 3-4.5 mm. wide at apex; keel 10-15 mm. long, appendage small, maculate or immaculate; pod 8-16 mm. long, erect, sessile, pilose, with a beak about 5 mm. long, partially two-loculed by intrusion of the ventral suture. (Barneby, 1952; Welsh, 1967).

The taxonomic category assigned to these variants has varied considerably in the literature. For the most part,

PLATE 1.

Type specimen of *Oxytropis campestris* (L.) DC.

HERBARIUM LINNAEANUM

Form of Savage Catalogue entries:

Some of the specific epithets and numbers are printed in **solid type**, *but solely as a help to the eye in tracing named specimens.* When these are not followed by the writer's name in square brackets they are written on the sheets by Linnaeus. Apart from everything enclosed in square brackets, all inscriptions in roman type are written by Linnaeus. The inscriptions by all other writers are printed *in italics.*

Where the same writer is responsible for the inscriptions both before and after his name, two ,,collons are used to show this,—e. g. [:m.Sm:].

Inscriptions at the top of a sheet are followed by the sign / ; those on the verso are preceded by the sign //.

The sign ▭ is used for "Label"; and a + sign before a writer's name means that the ensuing inscription is an addition to the one that precedes it.

No. 986.81

ASTRAGALUS

81 **Astragalus 30 monogynia** Orlaya. Astragalus, trigonocarpus foliis, non nervosis, floribus luteis. Amen. shot. 127. [+Sm:]?
Astragalus scandens, foliis pennatis, calyce et fructu villosis. Hall. fior. 367. t.13. [+Sm:]?
Habitat in Uralensibus montibus. [+Sm:]?

MAP 1.

Distribution of *Oxytropis campestris* (L.)DC. in northwestern North America based on Barneby (1952), Welsh (1967), and Hultén (1968)

var. *columbiana* (St.John) Barneby

var. *cusickii* (Greenm.) Barneby

var. *dispar* (A.Nels.) Barneby

var. *jordalii* (Porsild) Welsh

170
180
170
160
140
100
60
40
30
20
60
50
40
30
20
10

MAP 2.

Distribution of *Oxytropis campestris* (L.)DC. in northwestern North America based on Barneby (1952), Welsh (1967), and Hultén (1968)

var. *davisii* Welsh

var. *gracilis* (A.Nels.) Barneby

var. *varians* (Rydb.) Barneby

170
180
170
160
140
100
60
40
30
20
60
50
40
30
20
10

the plants of the New World have been held varietally distinct from *Oxytropis campestris* (L.)DC. In 1871, Watson recorded *O. campestris* as ranging from the arctic to Colorado while Bunge (1869) accepted the species as west European, east Asian, and western North American, noting, however, that the latter differed somewhat in stature and habit. Gray's revision (1884) excluded typical *O. campestris* from the American flora for the first time. The material which had been so named previously was divided into a western arctic *O. leucantha* and a new species, *O. monticola*, largely cordilleran and ochroleucous flowered. During the present century, the most western and Rocky Mountain forms have been variously segregated by different workers. Thus, in northwestern North America, where Watson could distinguish only *O. campestris sensu* Linneus, and Asa Gray only *O. monticola*; Nelson (1899), St. John (1928) and others collectively delineated fourteen species. This fact, coupled with the shifting back and forth between the genera *Astragalus* and *Oxytropis*, *Aragallus* and *Spiesia*, created an abundance of disordered synonyms and overall taxonomic confusion.

Barneby (1952) favored a return to the concept of an American *O. campestris*. He argued that while *O. campestris* in its original and narrowest sense is absent from the New World, the European and American plants can reasonably be ranked as geographic populations within a polymorphic,

circumboreal species, a view shared by Hultén (1967, 1968). Their "fundamental similarities" in structure and texture of the pod, in "flower", as well as orientation or amount of vestiture, indicated to Barneby the "inevitable acceptance" of an American *Oxytropis campestris* (L.)DC. In northwestern North America, he recognized five races (treated in the category of *varietas*) differentiated on the basis of petal colour, leaflet number, habitat, and stipule vestiture and ornamentation (see Tables 1 and 2).

Barneby's revision contributed greatly towards a stabilization of the nomenclature for the *O. campestris* complex and his species delimitations have been widely accepted. More recently, a number of authors have contributed to the taxonomy in this complex. Broadening Barneby's (1952) species concept, Welsh (1963) described two new varieties after examination and collection of specimens from British Columbia, the Yukon, and Alaska. One of these taxa, *jordalii*, had previously been described by Porsild (1951) as a new species confined to Alaska and the Yukon; it was accorded subspecific status by Hultén (1967). Thus, the examination of material using morphological criteria has resulted in the recognition of seven geographically and morphologically distinct subspecific taxa in *O. campestris* by Barneby (1952) and Welsh (1963).[2] Their

[2]Boivin (1967),in a rather cursory treatment of the *O. campestris* complex, recognized still another variety (var. *cervinus* (Greene) Boivin) characterized vaguely

TABLE 1.

Classification of the *Oxytropis campestris* (L.)DC. complex in Northwestern North America based on Barneby (1952) and Welsh (1963)

Oxytropis campestris (L.)DC var. *varians* (Rydb.) Barneby
Oxytropis campestris (L.)DC var. *gracilis* (A.Nels.) Barneby
Oxytropis campestris (L.)DC var. *cusickii* (Greenm.) Barneby
Oxytropis campestris (L.)DC var. *dispar* (A.Nels.) Barneby
Oxytropis campestris (L.)DC var. *columbiana* (St. John) Barneby
Oxytropis campestris (L.)DC var. *jordalii* (Porsild) Welsh
Oxytropis campestris (L.)DC var. *davisii* Welsh

TABLE 2. Diagnostic Characters of the Taxa in the *Oxytropis campestris* (L.)DC. Complex in Northwestern North America (based on Barneby 1952, and Welsh 1963)

TAXA	DISTINCTIVE FEATURES
var. *varians* (Rydb.) Barneby	stipules with clavate processes; flowers white or ochroleucous; Alaska, Yukon, N.W.T.
var. *gracilis* (A.Nels.) Barneby	numerous leaflets (17-33);uniformly yellowish corolla; prairie habitats in the north-central states, prairie provinces, locally in B.C. and Washington
var. *dispar* (A.Nels.) Barneby	polychrome racemes and flowers; coriaceous pod texture; prairie habitats in North Dakota
var. *columbiana* (St.John) Barneby	whitish corolla; maculate keel; robust plants of riparian habitats in Washington and Montana
var. *cusickii* (Greenm.) Barneby	few leaflets/leaf (7-17); few flowers/raceme; low statured plants of alpine and sub-alpine meadows in central and northern Rocky Mts.
var. *jordalii* (Porsild) Welsh	pinkish or purplish corolla; small flowers (12 mm.); few flowers/raceme (6-14); alpine and arctic tundra habitats in Alaska, western N.W.T., Yukon, locally to Alberta
var. *davisii* Welsh	numerous verticellate leaflets (31-51); purple corolla; streamside habitats in northeast B.C.

classification of the complex is presented in Table 1. A major aim of this research project was to obtain new systematic information on several cryptic characters (for example, chromosome number, flavonoid glycosides) and use these data to test the conclusions of Barneby (1952) and Welsh (1963).

Prior to this study, biosystematic studies of *O. campestris* have been confined to cytological observations by a few workers; their published and unpublished chromosome counts are listed in Table 3. Published data indicate the presence of at least three chromosome numbers in *O. campestris*: 2n=32 (Ledingham, 1957; Knaben, 1968), 2n=48 (Ledingham, 1960), and 2n=>60 (Johnson and Packer, 1968). These data also suggest that there is no extant diploid race (2n=16); only a tetraploid (32), hexaploid (48), and an octoploid race or higher (>60) occur in northwestern North America. The 2n=48 reported for var. *gracilis* (A. Nels.) Barneby (Ledingham, 1960) from Kamloops indicates that Barneby's characterization of that taxon may be oversimplified. East of the continental divide, however, var. *gracilis* has a consistent mitotic count of 2n=32 (Ledingham, 1957).

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by few leaflets and lowland habitats in British Columbia and Washington. This study did not examine the validity of Boivin's new combination due to its poor characterization and description and the fact that it is included in Barneby's var. *gracilis*.

TABLE 3.

Reported Chromosome Counts of the taxa in the *Oxytropis campestris* (L.)DC. Complex in Northwestern North America

Taxon	2n=	Locality	Reference
gracilis	32	Kananaskis Rd., Alberta	Mosquin, T., unpublished
gracilis	32	Olympic Park, Washington	Kruckeberg, A.R., unpubl.
gracilis	32	Burdick, Saskatchewan	Ledingham, G.F. 1957
gracilis	32	Crestwynd, Saskatchewan	"
gracilis	32	Regina, Saskatchewan	"
gracilis	32	Cypress Lake, Saskatchewan	"
gracilis	32	Moosomin, Saskatchewan	"
gracilis	48	Kamloops, B.C.	Ledingham, G.F. 1960
jordalii	32	White Mts., Alaska	Knaben, G. 1968
varians	>60	Ogotoruk Creek, Alaska	Johnson & Packer 1968

Other major objectives of the present study were to determine the distribution of the chromosome races in northwest North America and to identify and note the occurrence of the various flavonoid glycosides. No previous investigations of the flavonoids in *O. campestris* have been carried out although, as mentioned before, a few cursory examinations of Eurasiatic *Oxytropis* species were conducted. Flavonoid data have often proved invaluable in the resolution of taxonomic and evolutionary problems (for example, Adams and Turner, 1970). Their usefulness as "taxonomic markers" to aid the delimitation of generic and specific boundaries as well as their utility as "genetic markers" to indicate hybridization history is well documented in the literature (Peckett, 1959; Alston and Turner, 1963; Harborne, 1969). In addition, Denford (1973) and Packer (unpublished) have noted their potential as "historical markers" where refugial boundaries or migrational pulses could be indicated by flavonoid distribution.

In summary, seven morphologically distinctive and allopatric subspecific taxa are currently recognized in *Oxytropis campestris* (L.)DC. in northwestern North America by Barneby (1952) and Welsh (1963). There is evidence (Ledingham, 1957, 1960; Johnson and Packer, 1968) that this taxon represents a mature polyploid complex (Stebbins, 1971), possibly comprised of several species (Davis and

Heywood, 1963). For organizational and historical reasons, the data have been gathered and the results presented following the taxonomy of Barneby (1952) and Welsh (1963). In addition, a newly discovered chromosome race (2n=96) has served a similar organizing function.

CHAPTER 2

MATERIALS AND METHODS

Collections and Field Studies:

Field studies were undertaken to obtain plant material for laboratory and herbarium studies and to make ecological and breeding system observations, for example, substrate preference and possible hybridization. Collections of *Oxytropis campestris* (L.)DC were made throughout as much of its known range as possible (Barneby, 1952; Welsh, 1967) in northwestern North America. Material was obtained from twenty-six localities and included representative specimens of all seven taxa. Pressed herbarium specimens, air-dried and bagged material (for use in chemical studies), and live plants (for cytological, breeding system, and growth chamber studies) were collected for study.

Cultivation:

Live plants, transplanted into five-inch pots and grown in the University of Alberta greenhouses, were maintained under a diurnal temperature range of 10°-16°C with a relative humidity of 60% and a 16 hour photoperiod using natural lighting in the summer with supplemented light when required. Chlorotic plants were fertilized using a solution of 20-20-20 NPK fertilizer.

Further transplanting was often carried out due to root overcrowding and poor water retention of the native soils. Aphid and fungal infestations were treated using standard fungicides and insecticides.

Herbarium Studies:

Morphological and distributional studies were carried out on living and herbarium specimens from the following herbaria: University of Alberta, Edmonton (ALTA); Brigham Young University, Provo (BRY); the Gray Herbarium of Harvard University, Cambridge (GH); National Museum of Canada, Ottawa (CAN); University of Montana, Missoula (MONTU); University of Washington, Seattle (WTU); University of Calgary (UAC); Rocky Mountain Herbarium, Laramie (RM); United States National Museum, Washington, D.C. (US); and the University of Saskatchewan, Regina (USAS). The abbreviations used are those listed in Index Herbariorum (Holmgren and Keuken, 1974).

Guard Cell Measurements:

Various workers have found a correlation between cell size and ploidy level (Sax and Sax, 1937; Stebbins, 1971). In an effort to distinguish the chromosome races of *Oxytropis campestris* by cell size, measurements of epidermal guard cells were made. Leaves were soaked in boiling water for five minutes, the lower epidermis was then peeled off and placed on a microscope slide in a drop of water. Measurements were made using a micro-

meter eyepiece on an American Optical microscope (240X).

Cytological Studies:

Mitotic chromosome counts were made from actively growing root tips using the procedures of Tijo and Levan (1950) with slight modifications. Root tips were immersed in a 0.002 molar solution of 8-hydroxyquinoline (0.116 gm. in 400 mls. of water) for 2-3 hours at 13°-16°C; washed in distilled water for five minutes; then transferred to a watch glass and stained for thirty minutes in a solution of acetic orcein and 1N HCl (9:1). The solution was warmed over a bunsen burner 8-10 times during a thirty minute period. The tips were next placed on a slide in a drop of 45% acetic acid and a coverslip applied; then washed and made semi-permanent by ringing the coverslip with a mixture of gum mastic and paraffin wax (1:1). Chromosome counts were made under the oil immersion objective (1000X) of an American Optical microscope with a green filter. Several of the preparations were drawn using a camera lucida apparatus; these drawings were used in examination of chromosome morphology. Voucher specimens were deposited in the herbarium at the University of Alberta (ALTA).

Chemical Studies:

Identification of the flavonoid glycosides of five populations of *Oxytropis campestris* was carried out. In addition to the identification of the glycosides in these

five populations, chromatographic profiles of twenty-four populations were compared.

Above ground plant organs used in flavonoid extraction were collected in the field and dried in paper bags. Prior to chemical analysis, the collections were sorted to remove any contaminants. Stems, flowers, and leaves were uniformly used for extraction in every population sampled. Flavonoids were extracted using a blender; approximately 20 gm. (dry weight) of plant material were ground for 15 minutes in 500-700 mls. of 80% ethanol. The extract was then vacuum filtered through several layers of cheesecloth followed by Whatman #1 filter paper, then reduced in a rotoevaporator or flash evaporator under vacuum to 10-20 mls. Chlorophyll, other photosynthetic pigments, and lipids were removed by partitioning with multiple aliquots of petroleum ether (B.P. 60°-64°C). This extract will hereafter be referred to as the stock solution.

To identify the flavonoid aglycones, 10 mls. of the stock solution was combined with an equal amount of 2N HCl and refluxed at 110°C for three hours. The aglycones were then partitioned against ether, evaporated to dryness, and redissolved in a minimum volume of spectrograde methanol. Subsequently, they were spotted in varying concentrations on half sheets (23 X 57 cms.) of Whatman 1MM chromatography paper. Descending chromatogra-

phy was then carried out using three solvent systems: BAW (n-butanol-acetic acid-water, 4:1:5 upper phase), forestal (acetic acid-water-concentrated HCl, 30:10:3), and saturated phenol (phenol-water, 4:1). Identifications were made by comparison of R_f's with those reported by Harborne (1967, 1973) and Ribereau-Gayon (1972). UV spectral analysis was also carried out on certain purified aglycones; procedures as well as analysis of the data were based on Mabry *et al* (1969).

Seikel *et al* (1966) have reported that C-glycoflavonoids remain in the aqueous sugar layer after acid hydrolysis and ether extraction of the aglycones. To check for possible C-glycoflavonoids in the stock solution, the aqueous sugar layer was further extracted against amyl alcohol (Harborne, 1973). The amyl alcohol layer was then evaporated to dryness, redissolved in minimum methanol, and spotted on half sheets of Whatman 1MM paper. Descending chromatography of these sheets was then carried out in BAW, 15% acetic acid, and water.

Separation of the flavonoids of the stock solution was carried out on Whatman 3MM chromatography paper. To determine the optimum concentration for separation, varying volumes of the stock solution were spotted on 3MM paper and chromatographed descendingly in BAW for 16-19 hours. The sheets were then air-dried, rotated 90°, then run in 15% acetic acid for 6-8 hours. The chromato-

grams were viewed under UV light (3660Å) to determine efficiency of separation. The concentration which yielded the best separation was then used in the further isolation procedures.

Five to nine drops of the stock solution were spotted on at least forty-eight sheets of Whatman 3MM paper and chromatographed in BAW and 15% acetic acid according to the procedures outlined above. The chromatograms were then viewed under UV light in the presence and absence of fuming NH_3. Spots resolved under either of these conditions were circled and their colors noted. To test for the presence of flavonoids, one sheet was sprayed with Benedict's reagent (positive yellow reaction). Another sheet, used for the detection of phenolics, was treated with a 3% aqueous solution of ferric chloride-ferricyanide (positive blue reaction)[3]. Spots which yielded positive reactions to both treatments were cut out from the remaining sheets and eluted in 90% methanol. These solutions were evaporated to dryness and redissolved in minimum methanol.

To check flavonoid purity, the solutions were spotted on full sheets of Whatman 1MM paper and run, in the usual manner, in BAW and 15% acetic acid. Those solutions which were found to consist of more than one gly-

[3] Chromatograms were dipped in a solution containing equal amounts of ferric chloride and ferricyanide stains diluted 1:10 with water, then dipped in a 10% solution of HCl and washed with water.

coside (as indicated by the presence of two or more spots) were then streaked on Whatman 3MM paper in the solvent system which yielded the best separation.

The isolated flavonoids were identified using the procedures of Mabry *et al* (1969). The compounds were spotted on half sheets of Whatman 1MM paper until a yellow colour was visible. Descending chromatography was then carried out in four solvent systems: BAW, 15% acetic acid, water, and saturated phenol. R_f's in each of the four solvent systems were calculated for each of the unknowns and compared with those reported by Harborne (1967) and Ribereau-Gayon (1972). Approximately 10 µl of a 10^{-3} M solution of rutin (quercetin 3-O-rhamnosylglucoside) in methanolic solution was spotted on each sheet to serve as a reference; R_f's of the isolated compounds were corrected with respect to rutin.

UV spectral analysis using a Unicam SP 1800 spectrophotometer was carried out on each unknown using the procedures of Mabry *et al* (1969). These procedures included the comparison of methanol scans with those obtained after the addition of several diagnostic reagents to the methanolic solution. Scans were recorded for the effects of sodium methoxide, aluminum trichloride, aluminum trichloride plus hydrochloric acid, sodium acetate, and sodium acetate plus boric acid on the UV absorption of the compound in methanol.

The flavonoid glycosides were then hydrolyzed to their aglycone and sugar constituents by refluxing the methanolic solutions with an equal amount of 2N HCl at 100°C for twenty minutes to two hours depending on the suspected nature of the glycoside linkage (Ribéreau-Gayon, 1972). After hydrolysis, the solution was cooled and partitioned against 25 mls. of ethyl ether. The ether fraction, which contained the aglycone, was then evaporated to dryness, redissolved in minimum methanol, and chromatographed descendingly on Whatman 1MM paper in BAW, forestal, and saturated phenol. The aglycones were also chromatographed in 15% acetic acid to ensure that the sugar had been liberated during hydrolysis.

The lower aqueous layer contained the sugar component of the flavonoid glycosides. Identification of the flavonoid sugars was carried out using the procedures of Ribéreau-Gayon (1972). Neutralization of this acidic solution (although demonstrated experimentally to be unnecessary for purposes of identification) was carried out on approximately half of the isolated flavonoid sugars by using a 10% solution of di-n-octylmethylamine v/v in chloroform. Twenty-five mls. of this solution was partitioned against the acidic aqueous sugar fraction; the lower phase, containing the neutralized sugar solution, was then evaporated to dryness. The sugars were then redissolved in a minimum amount of 80% methanol and spot-

ted (two spots side by side) on half sheets of Whatman 1MM paper with the lower edge serrated. Five µl of a 0.5% solution of D-glucose in 10% isopropanol was added to one of these spots. In addition, a third solution, consisting of a mixture of five common sugars (glucose, rhamnose, xylose, galactose, arabinose) in 10% isopropanol, was applied next to the previously mentioned spots. Descending chromatography was then carried out in 80% isopropanol for 36 hours. Next, the sheets were air-dried, dipped in aniline hydrogenphthalate reagent, and heated in an oven at 55°C for twenty minutes in order to detect the sugars present. R_g's were calculated for each sugar and colour reactions compared with those reported by Zweig and Sherma (1972).

After the identification of the compounds of the five selected populations was completed, a chromatographic analysis of the spot patterns of twenty-four other populations was conducted. About 10 gms. dry weight of above ground flowering material was ground up with about 250 mls. of 80% ethanol. Concentration of the extract and determination of the optimum concentration for separation of the flavonoids were undertaken in the manner previously described. After the detection for phenolics and, more specifically, for flavonoids was carried out, the spot patterns and colour properties were noted. This information was then compared to the master

chromatogram in order to determine the distribution of the identified flavonoid glycosides.

CHAPTER 3.

RESULTS

Morphological and Phytogeographical Studies:

Examination of specimens revealed seven morphologically and geographically distinct taxa which, to a large extent, correspond to the seven varieties recognized by Barneby (1952) and Welsh (1963). The seven taxa were found to differ most significantly in habitat, leaflet number, stipule vestiture, number of flowers per raceme, pod texture, as well as corolla colour and length of the keel. The morphological differences are summarized in Table 4; they represent both vegetative and reproductive phases of the life cycle. Propagation in controlled environment facilities has indicated that these characters are not affected by varying environmental factors and therefore reflect genotypic differentiation.

Cytological Studies:

Cytological investigation confirmed the observation of Ledingham (1960) who noted that more than one chromosome number was present in *Oxytropis campestris* (L.)DC. *sensu lato*. Indeed, the data from the present study (Table 5) indicate that at least three chromosome numbers (32, 48, 96) are present in the species as defined by Barneby (1952), Welsh (1963), and Boivin (1967). These

TABLE 4.

Comparative morphological characters of the taxa in the *Oxytropis campestris* (L.)DC. complex in northwestern North America

Organ	Character	Taxa							
		varians *ssp racs*	*ssp racs*	*gracilis*	*disper*	*cusickii*	*columbiana*	*jordalii*	*davisii*
Leaves	Number of leaflets	13-45	13-23	17-33	17-25	7-17	11-17	9-25	31-51
Stipules	Dorsal Vesture	pilose, glabrate	pilose, glabrate	pilose, glabrate	densely pilose	thinly pilose, glabrate	pilose, rarely glabrate	thinly pilose, glabrate	thinly pilose, glabrate
	Marginal Vesture	ciliate, clavate processes	ciliate, clavate processes	ciliate, glabrate, clavate processes rare	ciliate, clavate processes rare	ciliate, rarely glabrate	ciliate, clavate processes rare	ciliate, clavate processes	ciliate, clavate processes
Raceme	Number of flowers	10-25	8-15	6-30	8-15	6-15	6-28	6-14	10-16
Corolla	Colour	ochroleu-cous, whitish	ochroleu-cous, whitish	ochroleu-cous, whitish	ochroleu-cous, whitish, pink, purplish	ochroleu-cous	whitish	ochroleu-cous, pink, purple	pink, purple
	Keel length (mm.)	10-12.5	13-15	10-14	12.5-14	11-14	11-14	10-11	11-12
Pod	Texture	Chartaceous	Chartaceous	Char.	Char. to Coriaceous	Char. to Coriaceous	Chartaceous	Chartaceous	Char.

TABLE 5.

Chromosome Counts for the *Oxytropis campestris* (L.)DC. Complex in northwestern North America determined in the present study

Taxon	2n=	Locality
var. *columbiana* (St. John) Barneby	48	Glacier Park, Montana
var. *cusickii* (Greenm.) Barneby	48	Anaconda Wilderness, Montana
	48	Jasper Park, Alberta
	48	Prospect Creek Rd., Alberta
	48	Waterton Park, Alberta
var. *davisii* Welsh	32	mile 403, ALCAN Hwy., B.C.
var. *dispar* (A. Nels.) Barneby	32	Morton Co., North Dakota
var. *gracilis* (A. Nels.) Barneby	32	W. of Calgary, Alberta
	32	Kananaskis Rd., Alberta
	32	Black Hills, South Dakota

TABLE 5.(cont.)

Taxon	2n=	Locality
var. *gracilis* (A. Nels.) Barneby	32	Albany Co., Wyoming
	32	Broadview, Saskatchewan
	32	Glacier Co., Montana
	48	Olympic Park, Washington
var. *varians* (Rydb.) Barneby	48	Dempster Hwy., Yukon
	48	Tok Jct., Alaska
	48	Kluane Lake, Yukon
	48	Moose Pass, Alaska
	48	Inuvik, N.W.T.
	96	mile 307 TAPS Hwy., Alaska
	96	S. of Mt. McKinley Park, Alaska
var. *jordalii* (Porsild) Welsh	32	Prospect Creek Rd., Alberta
	32	Richardson Mts., N.W.T.

numbers represent the tetraploid (32), hexaploid (48), and dodecaploid (96) condition and indicate that *Oxytropis campestris* (L.)DC. consists of a eupolyploid series in northwestern North America. The collections from which these chromosome counts were obtained are listed in Table 6.

The morphological taxa are generally correlated with chromosome number. Two taxa, however, are known to have more than one number; the taxon *gracilis* has both 2n=32 and 2n=48 while the taxon *varians* has 2n=48 and 2n=96. Map 3 shows the distribution of the chromosome numbers in the taxon *varians*. These data represent published chromosome counts (Table 3), the author's chromosome counts (Table 5), as well as chromosme numbers inferred by guard cell measurements (Table 8).

Analysis of the karyotype was conducted after treatment with 8-hydroxyquinoline for only the taxon *cusickii* (2n=48) and the taxon *gracilis* (2n=32). Observations of chromosome morphology (Figure 1) indicate that the medium-sized chromosomes are of fairly uniform length with median or sub-median centromeres. This condition, as noted by Stebbins (1971), is characteristic of a symmetrical karyotype commonly associated with unspecialized members of a family or genus. This contrasts with the asymmetrical karyotype where arm ratios and the relative lengths of the different chromosomes are heterogeneous. Asymmetrical

TABLE 6.

Collections of which Chromosome Counts are Based

Alaska: WJE #249, Tok Junction, June 24, 1976; WJE #268, Moose Pass, June 26, 1976; WJE #281, S. of McKinley Park, June 28, 1976; WJE #299, mile 307, TAPS Hwy., July 3, 1976; WJE #306, mile 322, TAPS Hwy., July 4, 1976.

Alberta: WJE #001a, 004a, Prospect Creek Rd., Cadomin, August 28, 1976; WJE #025, 217, Whitehorse Creek, Cadomin, June 24, 1976; WJE #043a, Hwy. #1, W. of Calgary, August 13, 1976; WJE #053, 060, Kananaskis Rd., July 15, 1975; WJE #110, Signal Mt., Jasper Park, August 23, 1975; WJE #222, Prospect Creek Rd., Cadomin, June 16, 1976; WJE #452, Carthew Mt., Waterton Park, July 12, 1977.

British Columbia: WJE #342, 343, mile 403, ALCAN Hwy., July 9, 1976.

Montana: WJE #099a, 100a, Goat Flats, Anaconda Wilderness, August 11, 1976; WJE #387,389, Mud Creek, Glacier Park, August 13, 1976; WJE #442, Glacier Co., July 9, 1977.

North Dakota: WJE #177, 181, Glen Ullin, Morton Co., May 26, 1976.

Northwest Territories: WJE #471, 472, Dolomite Lake,

TABLE 6. (cont.)

Inuvik, July 5, 1977.

Saskatchewan: WJE #190, Broadview, May 27, 1976.

South Dakota: WJE #162, 169, 170, Hwy. #16, Custer Co., Black Hills, May 25, 1976.

Washington: WJE #354, 356, Hurricane Ridge, Olympic Park, August 6, 1976.

Wyoming: WJE #154, Albany Co., May 24, 1976.

Yukon Territories: WJE #237, Kluane Lake, June 24, 1976; WJE #321, mile 82, Dempster Hwy., July 6, 1976.

FIGURE 1.

Somatic Chromosomes of certain taxa in the *Oxytropis campestris* (L.)DC. complex in northwestern North America

Oxytropis campestris (L.)DC var. *gracilis* (A.Nels.) Barneby
WJE #043 near Morley, Alberta
2n=32

Oxytropis campestris (L.)DC var. *cusickii* (Greenm.) Barneby
WJE #452 Carthew Mt., Waterton Park, Alberta
2n=48

karyotypes are characteristic of the more advanced or specialized members of a supraspecific taxon.

Attempts to observe meiotic pairing following fixation of flower buds in acetic alcohol proved unsuccessful.

Guard Cell Measurements:

Guard cell measurements indicated: 1) a positive correlation between guard cell size and ploidy level in the two taxa (*gracilis* and *varians*) with two chromosome numbers; 2) no significant difference between the mean guard cell length of the different taxa sharing the same chromosome number; and 3) that guard cell length in all taxa was positively correlated with ploidy level.

Within the taxon *gracilis*, the mean guard cell length for the tetraploid was 11.71 microns (N=485) while the mean for the hexaploid was 14.24 microns (N=75). A student's *t*-test showed a significant difference (Sdx=0.04, *t*=42.7) between the two means at the 0.1% level. Similar statistical procedures demonstrated that the mean (13.18 microns) of the hexaploid of the taxon *varians* differed significantly (Sdx=0.039, *t*=50) from the mean guard cell length (16.06 microns) of the dodecaploid.

The five taxa with uniform chromosome numbers did not differ significantly when their mean guard cell lengths were compared to the means of other taxa sharing the same ploidy level. Thus the taxa *jordalii*, *davisii*, and *dispar* all share the same chromosome number (2n=32)

while their respective mean cell lengths are 11.48 microns (N=176), 11.91 microns (N=100), and 11.81 microns (N=75). Both 2n=48, the taxa *columbiana* and *cusickii* have means of 13.41 microns (N=77) and 13.62 microns (N=350) respectively.

Collective analysis of the guard cell length data indicated that cell length was significantly correlated with chromosome number. Table 7 lists the statistical results while Figure 2 illustrates the size frequency data graphically. Over two thousand measurements were taken.

TABLE 7.

Statistical comparison of guard cell length between ploidy levels in the *Oxytropis campestris* (L.) DC. complex in northwestern North America

Comparison	Standard Deviation between means (Sdx)	*t* value
2n=32 : 2n=48	0.024	41.6
2n=48 : 2n=96	0.033	55.75
2n=32 : 2n=96	0.034	83.0

The significant differences between mean cell lengths made possible the determination of ploidy levels from herbarium specimens (Table 8). Only those specimens

TABLE 8.

Herbarium Specimens from Which Chromosome Number has been Determined by Guard Cell Measurement

2n=	Locality	Collector(s)	Herbarium
32	Mt. Mansfield, B.C., Haines Rd.	J. Sias #19	CAN
32	Richardson Mts., N.W.T.	S.L. Welsh & J.K. Rigby #12062	BRY
32	mile 81, Dempster Hwy., Y.T.	R.T. Porsild #1486	CAN
32	Mackenzie Mts., N.W.T.	A.E. Porsild & A.J. Breitung #11817	CAN
32	Canol Rd., mile 111E, N.W.T.	V.C. Wynne-Edwards #8346	CAN
32	Wiseman, Alaska	H.M. Raup & A.J. Soper #9427	GH
32	Mackenzie Mts., N.W.T.	H. M. Raup & A.J. Soper #9449	GH
32	Juneau, Alaska	M. Williams #1397	GH
48	Brintnell Lake, N.W.T.	H.M. Raup & A.J. Soper #9427	ALTA
48	mile 81, Mackenzie Hwy., N.W.T.	S.S. Talbot #4630	ALTA
48	mile 22E, Canol Rd., N.W.T.	W.J. Cody & R.L. Gutteridge #7959	ALTA
48	Jago River, Alaska	J.E. Cantlon & W.T. Gillis #57-743	CAN
48	Chitina River, Alaska	H.M. Laing #125	CAN

TABLE 8. (cont.)

48	Jago River, Alaska	J.E. Cantlon & W.T. Gillis #57-1066	CAN
48	Lake Schrader, N. Slope, Alaska	L.A. Spetzman #518	CAN
48	Hayes River, N.W.T.	H.J. Scoggan #5893	CAN
48	Churchill, Manitoba	G.M. Keleher #31	CAN
48	Umiat, Alaska	I.L. Wiggins #13878	CAN
48	Umiat, Alaska	R.D. & M. Wood #421	CAN
48	Ewariege Lake, N.W.T.	V. Hawley #?	CAN
48	Richardson Mts., N.W.T.	J.G. Packer #1371	ALTA
48	Fairbanks, Alaska	E.Scaman #1654	GH
48	Churchill, Manitoba	A.E. Porsild #5480	GH
48	Firth R. & Mancha R., Alaska	E. Hulten #62767	BRY
48	Stevens Co., Wash.	H.T. Rogers #520	GH
48	Okanagan Co., Wash.	H. St. John #7703	GH
48	Savona, B.C.	C.L. Hitchcock & J. S. Martin #7396	GH
48	Mt. Wow, Wash.	J.W. Thompson #12578	GH
96	Ogotoruk Creek, Alaska	J.G. Packer #2582	ALTA
96	Cape Thompson, Alaska	R.D. & M. Wood #555	CAN

TABLE 8. (cont.)

96	Okpilak Lake, Alaska	J.E. Cantlon & W.M. Malcolm #58-0283	CAN
96	Richardson Hwy., Alaska	E. Scaman #4622	GH
96	Mt. McKinley Park, Alaska	E. Scaman #5103	GH
96	Gulkana, Alaska	E. Scaman #4547	GH
96	Curry, Alaska	E. Scaman #1617B	GH
96	Rapids Lodge, Alaska	E. Scaman #296	GH

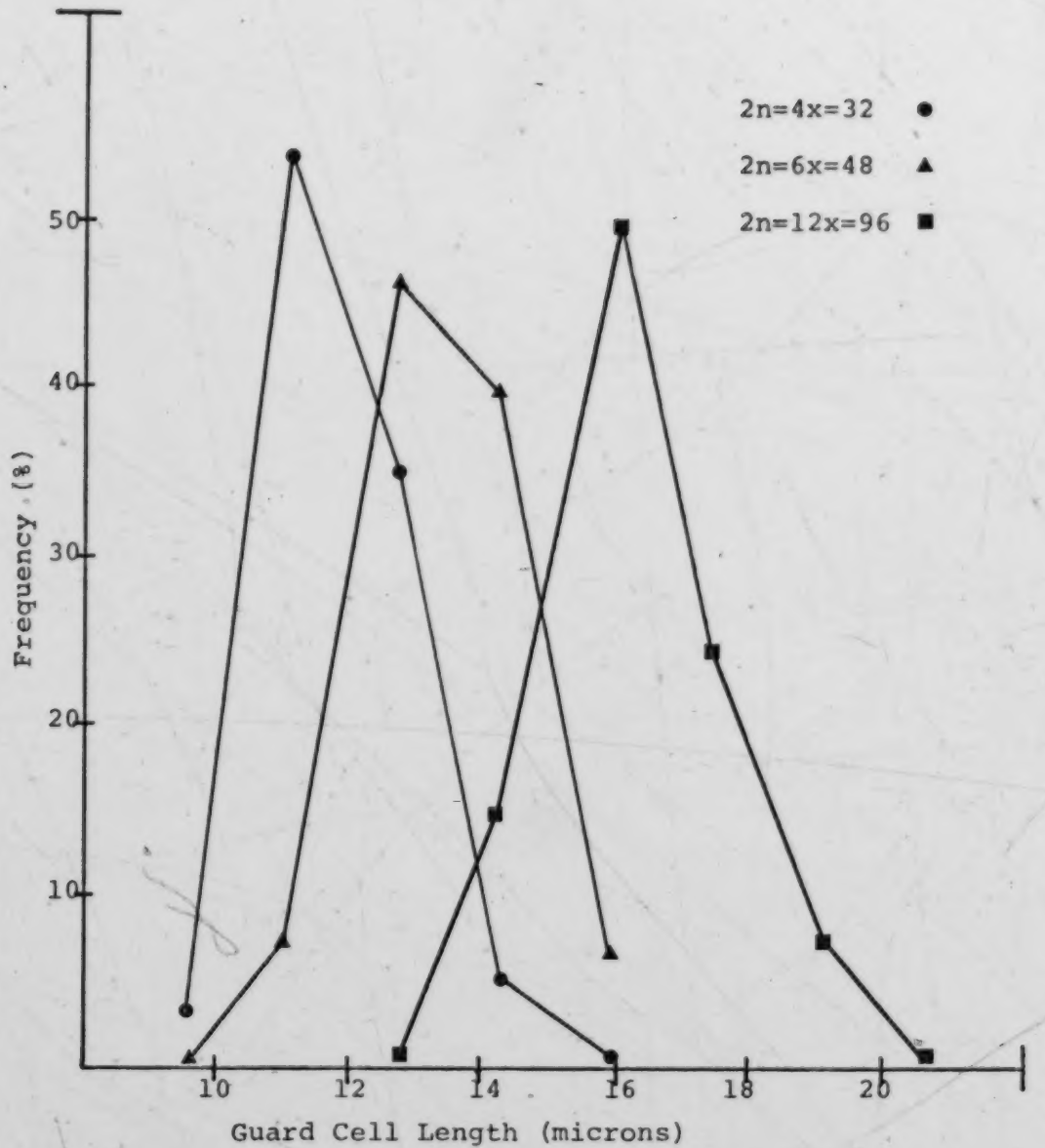


FIGURE 2. Guard Cell Length Frequencies in the *Oxytropis campestris* (L.)DC. Complex in Northwestern North America

in which the average cell length was within 0.75 microns of the predicted mean were used.

Chemical Studies:

The chemical aspects of this investigation involved detailed analysis of the flavonoid constituents in five populations. These five populations were deliberately chosen to represent four of the morphological taxa, the three ploidy levels, and material from glaciated and unglaciated regions of the continent. Figures 3-7 and Tables 9-13 show the fifty-eight compounds that were extracted, purified, and characterized using various chromatographic, hydrolytic, and optical procedures.

Comparison of these data revealed that at least thirty-three different flavonoid glycosides were present in the populations sampled (Figures 10-42). A total of seventeen flavone glycosides were found (Figure 8, Table 14) while the remaining sixteen compounds (Figure 9, Table 15) were flavonol glycosides. Apigenin and luteolin were the two flavone aglycones identified; similarly, there were only two flavonol aglycones: kaempferol and quercetin. Four glycosides had unidentified aglycone components.

Only three of the five populations examined contained glycosides of all four known aglycones. The sample population of the taxon *cusickii* lacked apigenin glycosides while that of the taxon *jordalii* lacked kaempferol glycosides.

FIGURE 3.

Master chromatogram of the flavonoid glycosides in *Oxytropis campestris* (L.)DC. var. *cusickii* (Greenm.) Barneby WJE #021, Prospect Creek Road, Alberta

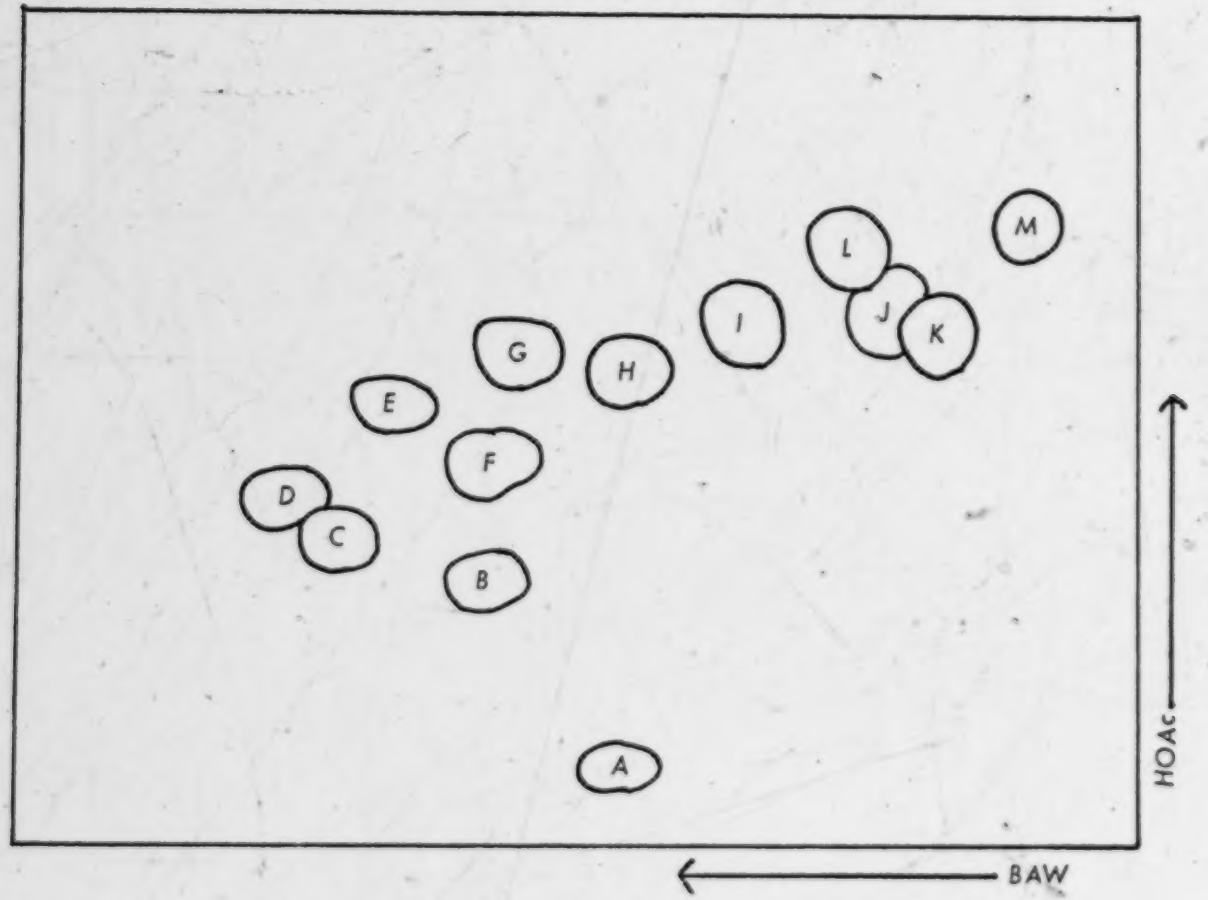


TABLE 9.

Flavonoid glycosides of *Oxytropis campestris* (L.) DC. var. *cusickii* (Greenm.) Barneby

WJE #021, Prospect Creek Road, Alberta

Compound	Colour UV/NH_3	R_f's X 100 Solvents				U.V. Spectral Data λ (in nm.) MeOH							Aglycone	Sugar(s)	Attachment
		BAW	H_2O	HoAc	PhOH	II	I	NaOMe I	$AlCl_3$ I	HCl I	H_3BO_3 I	NaOAc II			
A	p.y	47	02	11	56 38	256 270	346	56	79	-67	24	0	luteolin	glucose	7-O-glucoside
B	p.y	59	06	34	29	257 268sh	358	66	54	-48	16	17	quercetin	glucose	3-O-glucoside
C	p.y	70	09	38	70 41	256 268sh	358	60	48	-44	4	17	quercetin	glucose	3-O-glucoside
D	p.yg	76	13	43	68	268	306sh 351	55	48	---	5	6	kaempferol	glucose	3-O-glucoside
E	p.yg	66	23	53	62	267	350	60	50	---	4	8	kaempferol	glucose xylose	3-O-sambubioside
F	p.y	58	18	48	67 48	258 270sh	358	62	62	-58	12	18	quercetin	glucose xylose	3-O-sambubioside
G	p.yg	54	26	60	53	258 270sh	358	64	66	-62	18	14	quercetin	glucose xylose	3-O-diglucosyl- xyloside
H	p.yg	44	25	57	25	258 270sh	356	62	58	-54	12	10	quercetin	glucose xylose	3-O-diglucosyl- xyloside
I	p.y	36	38	61	47	276 286sh	344	70	54	---	18	0	?	?	?
J	p.y	24	43	65	44	256 270sh	358	64	72	-66	14	6	quercetin	?	?
K	p.y	19	30	62	28	258 268sh	358	72	62	-54	20	12	quercetin	glucose	3-O-glucose 7-O-glucoside
L	p.y	27	53	71	46	260 270sh	362	66	56	-52	18	8	quercetin	glucose xylose	3-O-sambubioside 7-O-glucoside
M	p.y	10	59	74	34	258 270sh	358	64	80	-72	20	8	quercetin	glucose	3-O-sophoroside 7-O-glucoside

p - purple, y - yellow, yg - yellow-green

FIGURE 4.

Master chromatogram of the flavonoid glycosides in *Oxytropis campestris* (L.)DC. var. *gracilis* (A.Nels.) Barneby WJE #048, Hwy. #1, West of Calgary, Alberta

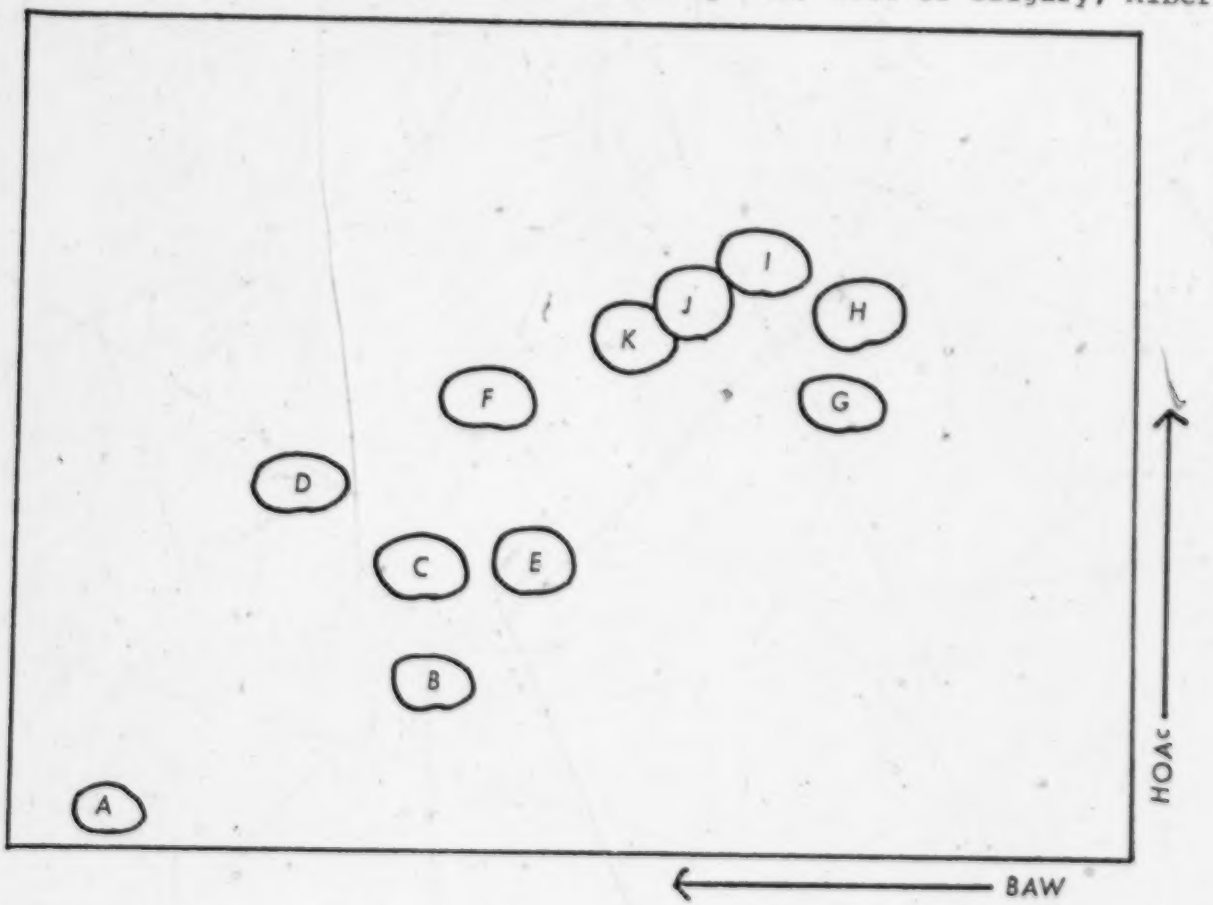


TABLE 10.

Flavonoid glycosides of *Oxytropis campestris* (L.) DC. var. *gracilis* (A.Nels.) Barneby

WJE #048, Hwy. #1, west of Calgary, Alberta

Compound	Colour UV/NH_3	R_f's X 100 Solvents BAW	H_2O	HOAc	PhOH	MeOH II	MeOH I	U.V. Spectral Data λ (in nm.) NaOMe I	$AlCl_3$ I	HCl I	H_3BO_3 I	NaOAc II	Aglycone	Sugar(s)	Attachment
A	P.yg	90	01	04	87	264	324	80	86	---	0	6	?	glucose	?
B	P.y	62	03	23	81	272	326	70	60	-36	12	0	apigenin	glucose rhamnose	7-O-rutinoside
C	P.y	63	10	36	79 60 46	258 268sh	360	70	52	-50	10	18	quercetin	glucose rhamnose	3-O-glucosyl-rhamnoside
D	P.yg	73	15	44	85 75	269	353	49	48	---	2	5	kaempferol	glucose	3-O-glucoside
E	P.y	54	52	33	29	258 268sh	356	65	56	-51	12	17	quercetin	glucose rhamnose	3-O-glucosyl-rhamnoside
F	P.yg	58	54	54	61	268	350	88	68	---	0	8	kaempferol	glucose rhamnose	3-O-rutinoside
G	P.yg	26	69	53	58	274	338	64	50	-40	12	10	?	glucose	?
H	P.y	24	51	66	61	259 270	338	86	66	-42	18	9	luteolin	glucose	7-O-triglucoside
I	P.yg	33	33	71	54	270	340	62	61	---	10	4	?	glucose rhamnose	?
J	P.yg	40	40	66	77	268	344	42	56	---	2	2	apigenin	glucose	7-O-triglucoside
K	P.yg	45	28	63	74	272 284	324	70	75	---	0	0	apigenin	glucose arabinose	7-O-vicianoside

P - purple, y - yellow, yg - yellow-green

FIGURE 5.

Master chromatogram of the flavonoid glycosides in *Oxytropis campestris* (L.)DC. var. *jordalii* (Porsild) Welsh WJE #223, Mt. Cheviot, Prospect Creek Road, Alberta

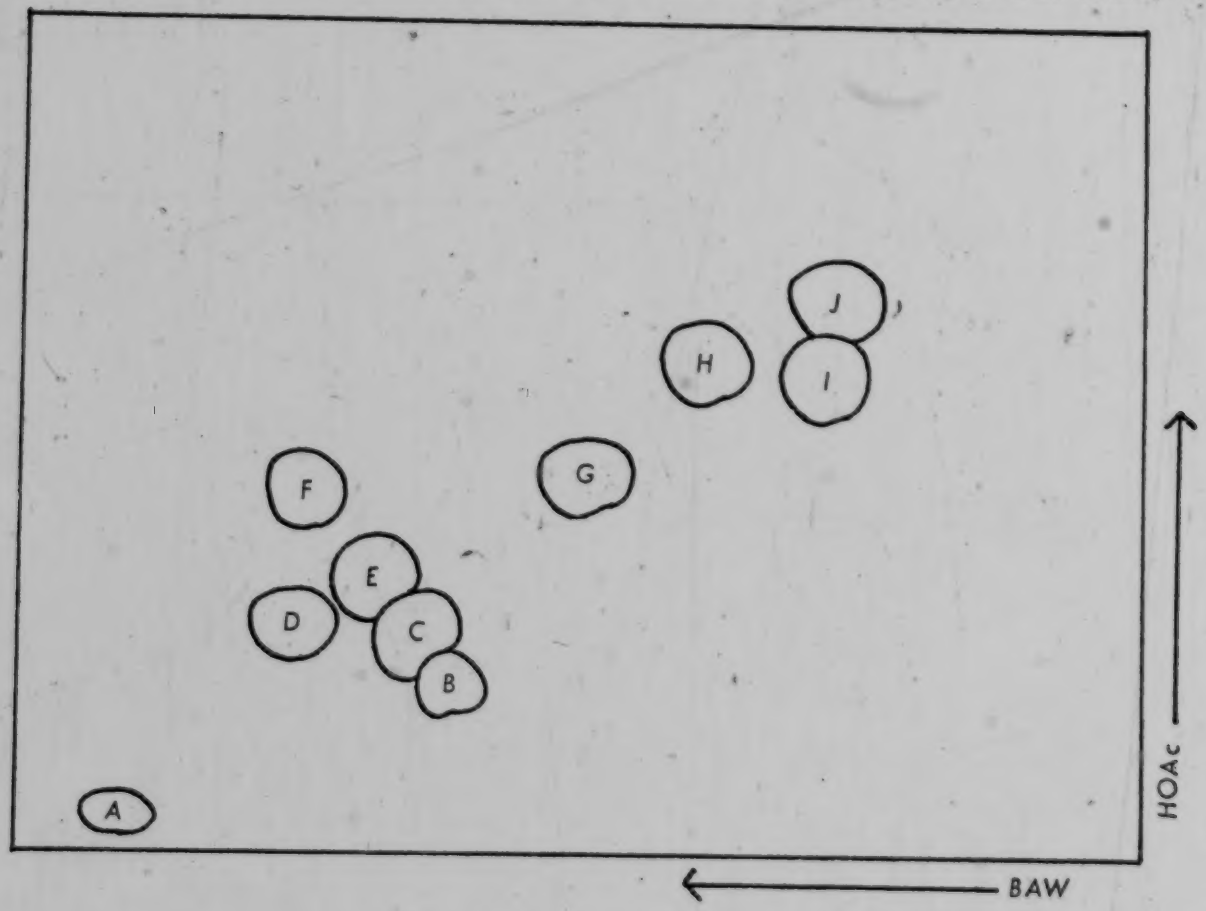


TABLE 11.

Flavonoid glycosides of *Oxytropis campestris* (L.) DC. var. *jordalii* (Porsild) Welsh

WJE #223, Mt. Cheviot, Prospect Creek Road, Alberta

Compound	Colour UV/NH_3	R_f's X 100 Solvents BAW	H_2O	HoAc	PhOH	U.V. Spectral Data λ (in nm.) MeOH II	MeOH I	NaOMe I	$AlCl_3$ I	HCl I	H_3BO_3 I	NaOAc II	Aglycone	Sugar(s)	Attachment
A	p.y	89	02	04	55	258 268sh	330	66	56	-44	0	16	?	glucose	?
B	p.y	60	03	22	80	270	330	66	56	---	0	0	apigenin	glucose	7-O-glucoside
C	p.y	62	12	27	78	270	324	64	60	---	4	8	apigenin	glucose	7-O-glucoside
D	p.y	74	08	28	78	256 268sh	352	66	52	-42	7	18	quercetin	glucose	3-O-glucoside
E	p.y	68	20	34	79	256 268sh	356	62	52	-46	7	18	quercetin	glucose rhamnose	3-O-glucosyl-rhamnoside
F	p.y	72	15	45	56	268	330	82	70	---	26	4	apigenin	glucose	7-O-diglucoside
G	p.y	48	25	48	66	258 270sh	334	94	72	-46	26	12	luteolin	glucose	7-O-diglucoside
H	p.yg	41	29	61	79	272	326	70	72	---	22	0	apigenin	glucose xylose	7-O-sambubioside
I	p.y	29	35	59	71	272	330	70	70	---	6	0	apigenin	glucose	7-O-triglucoside
J	p.yg	28	31	68	47	258 268sh	338	84	60	-38	20	10	luteolin	glucose	7-O-triglucoside

p - purple, y - yellow, yg - yellow-green

FIGURE 6.

Master chromatogram of the flavonoid glycosides in *Oxytropis campestris* (L.)DC. var. *varians* (Rydb.) Barneby WJE #250, East of Tok Jct., Alaska 2n=48

TABLE 12.

Flavonoid glycosides of *Oxytropis campestris* (L.) DC. var. *varians* (Rydb.) Barneby

WJE #250, east of Tok Jct., Alaska 2n=48

Compound	Colour UV/NH_3	R_f's X 100				U.V. Spectral Data λ (in nm.)							Aglycone	Sugar(s)	Attachment
		Solvents				MeOH		NaOMe	$AlCl_3$	HCl	H_3BO_3	NaOAc			
		BAW	H_2O	HoAc	PhOH	II	I	I	I	I	I	II			
A	p,yg	89	00	08	90	270	328	68	62	50	4	6	?	glucose	?
B	p,y	41	02	11	85	258							luteolin	glucose	7-O-glucoside
C	p,yg	64	03	23	61	268	324	68	64	---	8	2	apigenin	glucose rhamnose	7-O-rutinoside
D	p,yg	67	13	39	76 48	256	356	64	54	-48	6	18	quercetin	glucose	3-O-glucoside
E	p,y	51	52	39	25	258 270sh	334	84	80	-52	26	14	luteolin	glucose rhamnose	7-O-rutinoside
F	p,yg	72	12	49	55	260 270sh	350	58	51	---	4	17	kaempferol	glucose	3-O-glucoside
G	p,yg	74	15	51	61 47	269	350	64	58	---	11	4	kaempferol	glucose	3-O-glucoside
H	p,yg	50	33	54	70 44	258 270sh	358	61	52	-46	18	18	quercetin	glucose rhamnose	3-O-rutinoside
I	p,yg	43	35	67	46	270	324	68	74	---	8	4	?	glucose rhamnose	?
J	p,yg	30	29	62	61	258 268sh	330	98	76	-42	30	0	luteolin	glucose rhamnose	7-O-glucosyl-rutinoside
K	-,y	23	44	66	41	256 268sh	330	103	68	-40	24		luteolin	glucose	7-O-triglucoside

p - purple, y - yellow, yg - yellow-green

FIGURE 7.

Master chromatogram of the flavonoid glycosides in *Oxytropis campestris* (L.)DC. var. *varians* (Rydb.) Barneby WJE #310, mile 322, TAPS Hwy., Alaska 2n=96

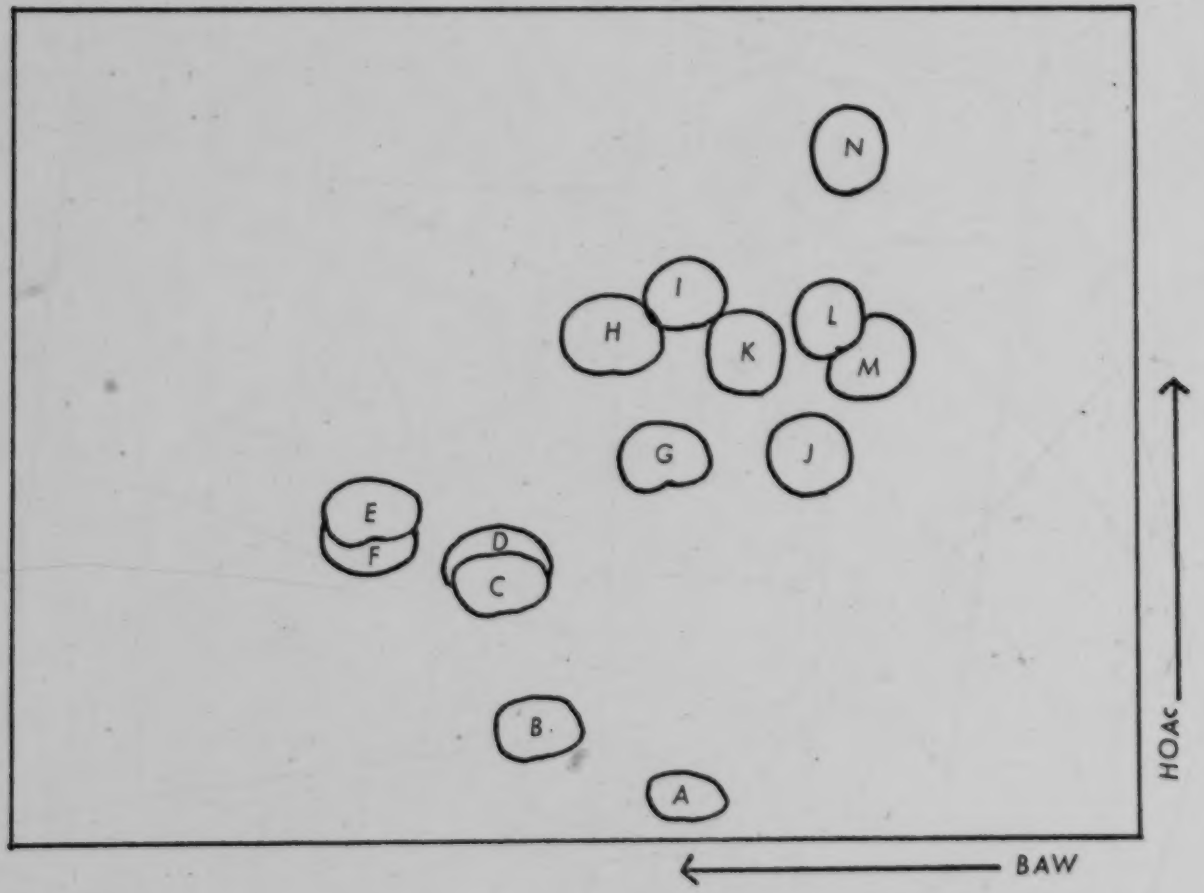


TABLE 13.

Flavonoid glycosides of *Oxytropis campestris* (L.) DC. var. *varians* (Rydb.) Barneby

WJE #310, mile 322, TAPS Hwy., Alaska 2n=96

Compound	Colour UV/NH_3	R_f's X 100 Solvents BAW	H_2O	HoAc	PhOH	U.V. Spectral Data λ (in nm.) MeOH II	I	NaOMe I	$AlCl_3$ I	HCl I	H_3BO_3 I	NaOAc II	Aglycone	Sugar(s)	Attachment
A	p,y	41	01	07	54	272 286sh				---		0	luteolin		7-O-glucoside
B	p,yg	54	02	15	83	268 274sh	330		53	---			apigenin	* glucose arabinose	7-O-vicianoside
C	p,y	57	14	32	75 51	258 268sh	356	58	64	-60	12	16	quercetin	glucose	3-O-glucoside
D	p,y	57	09	33	73 48	258 270sh	358	58	48	-44	4	18	quercetin	glucose	3-O-glucoside
E	p,yg	68	20	41	76	268	352	51	46	---	4	10	kaempferol	glucose	3-O-glucoside
F	p,yg	68	18	38	78	268	300 352	50	48	---	2	8	kaempferol	glucose	3-O-glucoside
G	p,y	42	35	47	74	256 268sh	358	60	50	-46	6	12	quercetin	glucose rhamnose	3-O-glucosyl-rhamnoside
H	p,yg	47	40	62	79	270	326	84	72	---	26	0	apigenin	glucose rhamnose	7-O-rutinoside
I	p,	40	26	57	78 67	270								glucose	?
J	p,	29	18	48	60	270	330							glucose	?
K	p,y	35	39	58	60	272	330	84	70	---	20	0	apigenin	glucose	7-O-triglucoside
L	p,	28	33	61	70	276						0		glucose	?
M	p,	25	48	59	60 39	258 282sh								glucose	?
N	-,	26	73	83	--	278 286sh						0		glucose	?

p - purple, y - yellow, yg - yellow-green

FIGURE 8.

Master chromatogram of the flavone glycosides of the *Oxytropis campestris* (L.)DC. complex in northwestern North America

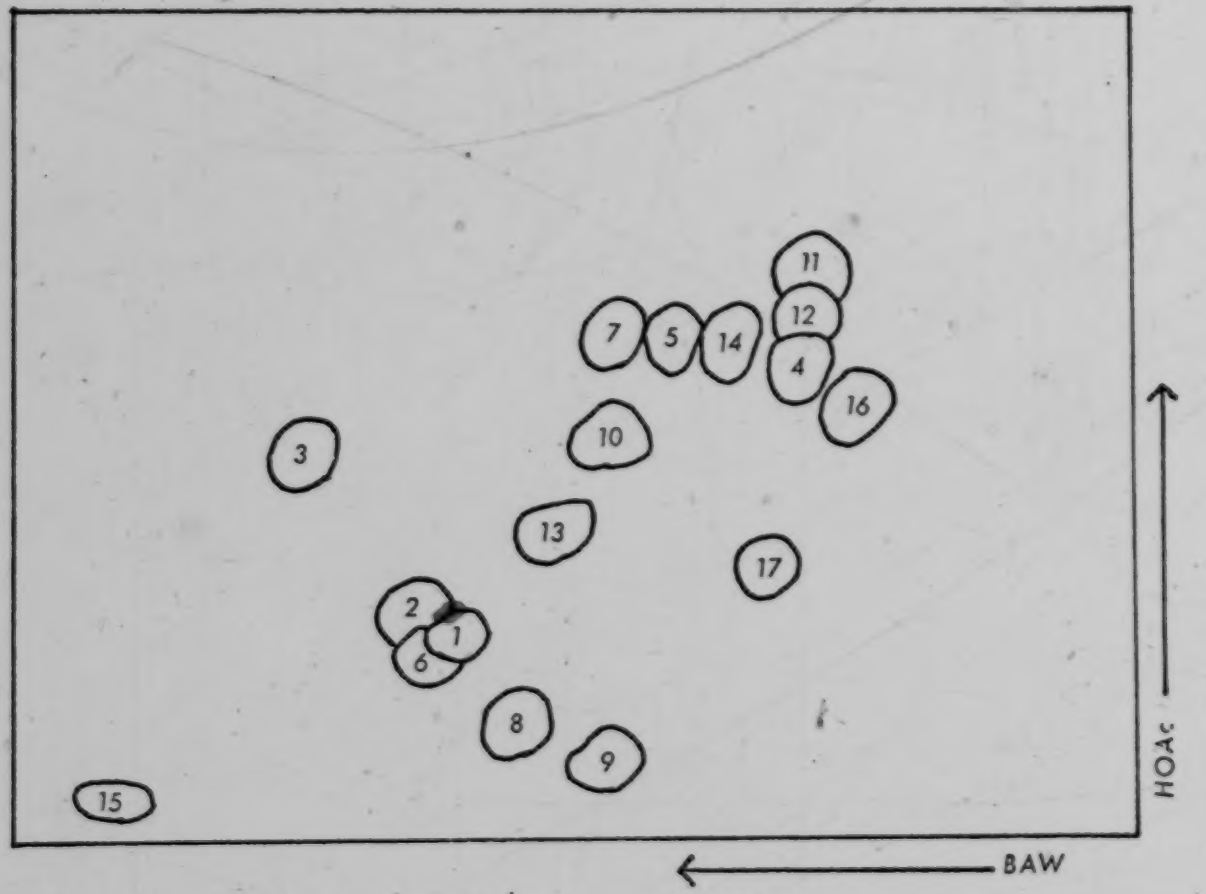


TABLE 14.

Flavone glycosides of the *Oxytropis campestris* (L.)DC. complex in northwestern North America

Compound Number	Colour UV/NH_3	Rf's X 100 Solvents				U.V. Spectral Data λ (in nm.) MeOH		NaOMe	$AlCl_3$	HCl	H_3BO_3	NaOAc	Aglycone	Sugar(s)	Attachment
		BAW	H_2O	HoAc	PhOH	II	I	I	I	I	I	II			
1	P.Y	60	03	22	80	270	330	66	56	---	0	0	apigenin	glucose	7-O-glucoside
2	P.Y	62	12	27	78	270	324	64	60	---	4	8	apigenin	glucose	7-O-glucoside
3	P.Y	72	15	45	56	268	330	82	70	---	26	4	apigenin	glucose	7-O-diglucoside
4	P.Y	29	35	59	71	272	330	70	70	---	6	-4	apigenin	glucose	7-O-triglucoside
5	P.Y	41	29	61	79	272	326	70	72	---	22	0	apigenin	glucose xylose	7-O-sambubioside
6	P.YG	62	03	23	81	272	326	70	60	---	8	8	apigenin	glucose rhamnose	7-O-rutinoside
7	P.YG	45	28	63	74	272 284	324	70	75	---	0	0	apigenin	glucose arabinose	7-O-glucosyl-vicianoside
8	P.YG	54	02	15	83	268	330		53	---			apigenin	glucose arabinose	7-O-vicianoside
9	P.Y	47	02	11	56 38	256 270	346	56	79	-67	24	0	luteolin	glucose	7-O-glucoside
10	P.Y	48	25	48	66	258 270sh	334	94	72	-46	26	12	luteolin	glucose	7-O-diglucoside
11	P.YG	28	31	68	47	258 268sh	338	84	60	-38	20	10	luteolin	glucose	7-O-triglucoside
12	P.YG	30	29	62	61	258 268sh	330	98			30	0	luteolin	glucose rhamnose	7-O-glucosyl-rutinoside
13	P.YG	51	52	39	25	258 268sh	334	84	80	-52	36	14	luteolin	glucose rhamnose	7-O-rutinoside
14	P.Y	36	38	61	47	276 286sh	344	70	54	---	18	-4	?	?	
15	P.Y	89	02	04	55	258 268sh	330	66	56	-44	0	8	?	glucose	
16	P.YG	26	69	53	58	274	338	64	50	-40	12	10	?	glucose	
17	P.YG	33	33	71	54	270	340	62	61	---	10	4	?	glucose rhamnose	

P - deep purple, Y - yellow, YG - yellow-green

FIGURE 9.

Master chromatogram of the flavonol glycosides of the *Oxytropis campestris* (L.)DC. complex in northwestern North America

TABLE 15.

Flavonol glycosides of the *Oxytropis campestris* (L.)DC. complex in northwestern North America

Compound Number	Colour UV/NH_3	R_f's x 100 Solvents				U.V. Spectral Data λ (in nm.) MeOH		NaOMe	$AlCl_3$	HCl	H_3BO_3	NaOAc	Aglycone	Sugar(s)	Attachment
		BAW	H_2O	HoAc	PhOH	II	I	I	I	I	I	II			
18	p.yg	76	13	43	68	260	351	55	48	---	5	6	kaempferol	glucose	3-O-glucoside
19	p.yg	66	23	53	62	267	350	60	50	---	4	8	kaempferol	glucose xylose	3-O-sambubioside
20	p.yg	58	54	54	61	268	350	80	68	---	0	8	kaempferol	glucose rhamnose	3-O-rutinoside
21	p.y	58	06	34	29	257 268sh	358	66	54	-48	16	17	quercetin	glucose	3-O-glucoside
22	p.y	57	14	32	75 51	258 268sh	354	60	66	-60	14	14	quercetin	glucose	3-O-glucoside
23	p.y	70	09	38	70 41	256 268sh	358	60	48	-44	4	17	quercetin	glucose	3-O-glucoside
24	p.y	19	30	63	20	258 268sh	358	72	62	-54	20	12	quercetin	glucose	3-O-glucose 7-O-glucoside
25	p.y	10	59	74	34	258 270sh	358	64	80	-72	20	8	quercetin	glucose	3-O-sophoroside 7-O- glucoside
26	p.y	58	18	48	67 48	258 270sh	358	62	62	-58	12	18	quercetin	glucose xylose	3-O-sambubioside
27	p.yg	54	26	60	53	258 270sh	358	64	66	-62	18	14	quercetin	glucose xylose	3-O-diglucosyl-xyloside
28	p.yg	44	25	57	25	258 270sh	356	62	58	-54	12	10	quercetin	glucose xylose	3-O-diglucosyl-xyloside
29	p.y	27	53	71	46	260 270sh	362	66	76	-52	18	8	quercetin	glucose xylose	3-O-sambubioside 7-O-glucoside
30	p.y	63	10	36	79 60 46	258 268sh	360	78	52	-50	10	10	quercetin	glucose rhamnose	3-O-glucosyl-rhamnoside
31	p.y	48	20	34	79	256 268sh	356	62	52	-46	12	18	quercetin	glucose rhamnose	3-O-glucosyl-rhamnoside
32	p.yg	50	33	54	70 44	258 268sh	358	62	52	-46	18	18	quercetin	glucose rhamnose	3-O-rutinoside
33	p.y	24	43	68	44	256 270sh	358	64	72	-66	14	6	quercetin	?	

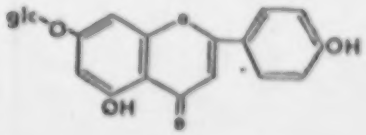
p - deep purple, y - yellow, yg - yellow-green

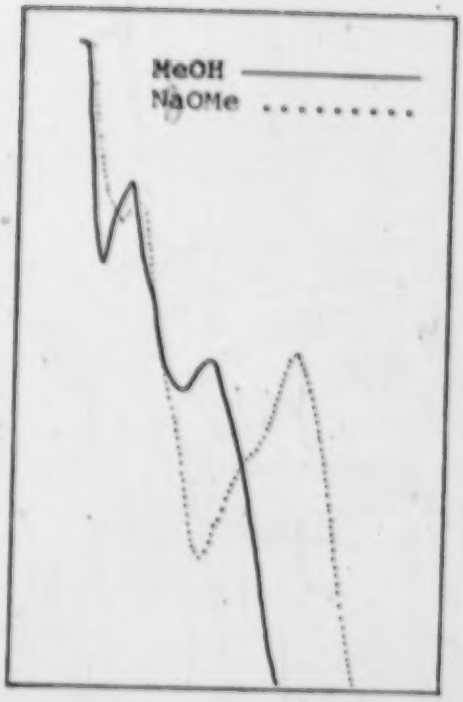
FIGURE 10.

Chromatographic and spectral data for Apigenin 7-O-glucoside

#1 Apigenin 7-O-glucoside

isomer #1





Chromatographic Data

	Rf Values			Spot Colour	
BAW	H_2O	HoAc	PhOH	UV	UV/NH_3
60	03	22	80	ppl	ylw

UV Spectral Data

MeOH	270, 330
NaOMe	275, 358sh, 392
$AlCl_3$	278, 346, 386
$AlCl_3$/HCl	278, 342, 384
NaOAc	270, 388
H_3BO_3	272, 330

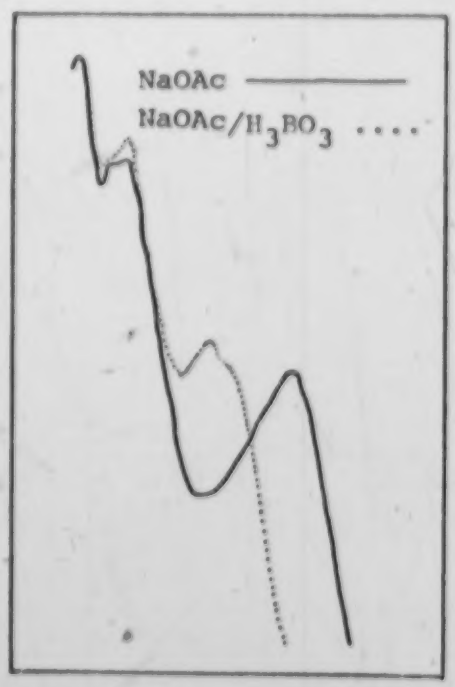
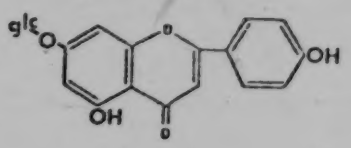


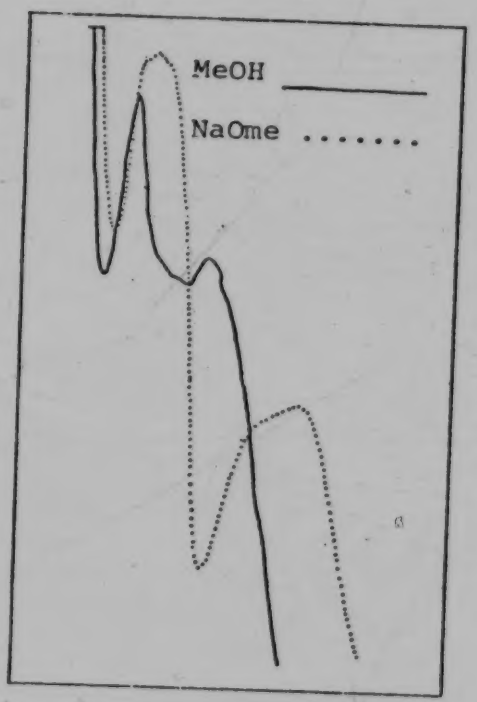
FIGURE 11.

Chromatographic and spectral data for Apigenin 7-O-glucoside

#2 Apigenin 7-O-glucoside

isomer #2



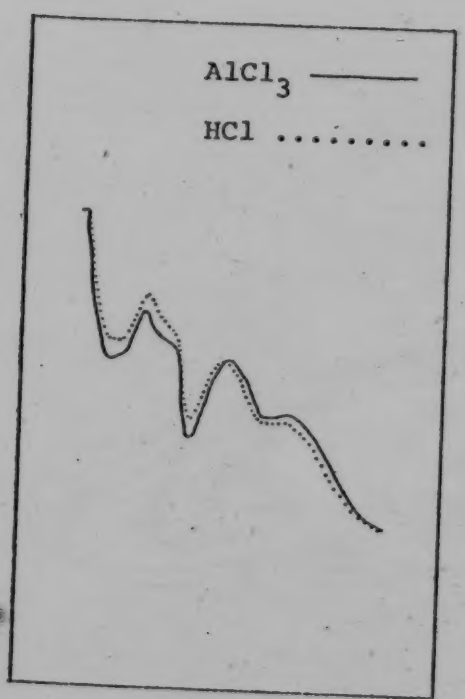


Chromatographic Data

Rf Values				Spot Colour	
BAW	H_2O	HoAc	PhOH	UV	UV/NH_3
62	12	27	78	ppl	ylw

UV Spectral Data

MeOh	270, 324
NaOMe	280, 358sh, 384
$AlCl_3$	278, 302sh, 341, 384
$AlCl_3$/HCl	280, 302sh, 336, 384
NaOAc	278, 366
H_3BO_3	272, 328



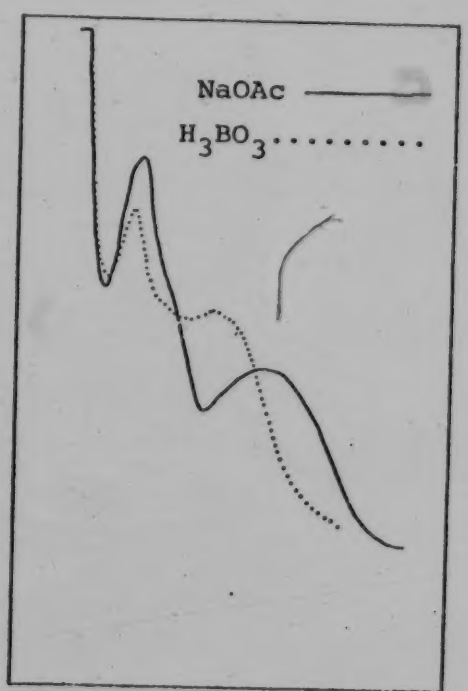
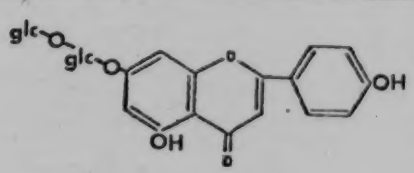


FIGURE 12.

Chromatographic and spectral data for Apigenin 7-O-diglucoside

#3 Apigenin 7-O-diglucoside

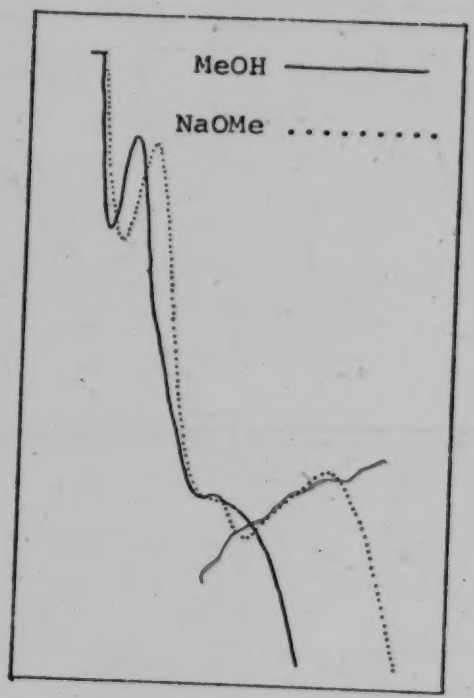


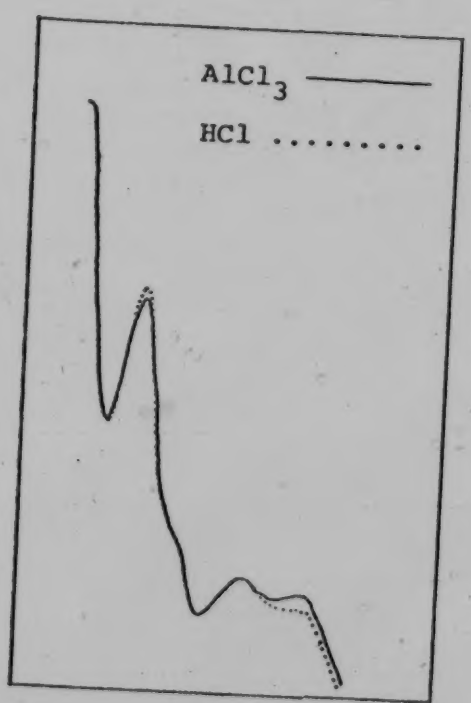
Chromatographic Data

	Rf Values			Spot Colour	
BAW	H_2O	HoAc	PhOH	UV	UV/NH_3
72	15	45	56	ppl	ylw

UV Spectral Data

MeOH	268, 330
NaOMe	280, 334, 412
$AlCl_3$	276, 306sh, 354, 400
$AlCl_3$/HCl	276, 306sh, 354, 400
NaOAc	272, 378
H_3BO_3	268, 356





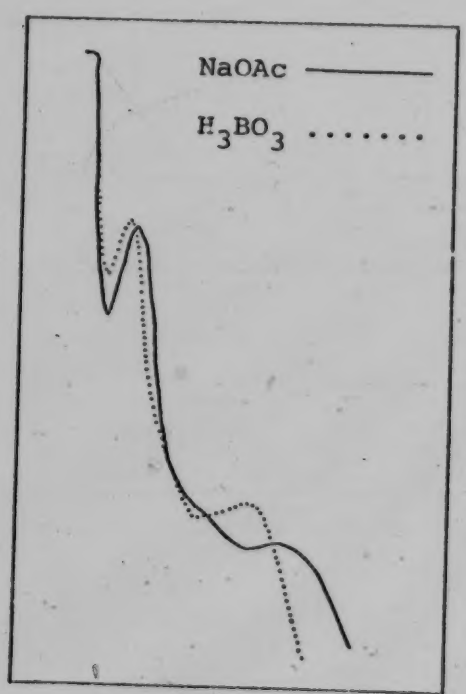
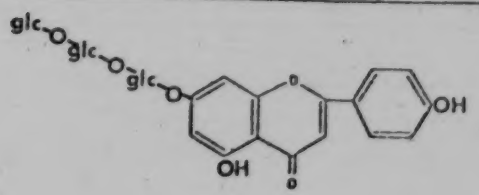


FIGURE 13.

Chromatographic and spectral data for Apigenin 7-O-triglucoside

#4 Apigenin 7-O-triglucoside

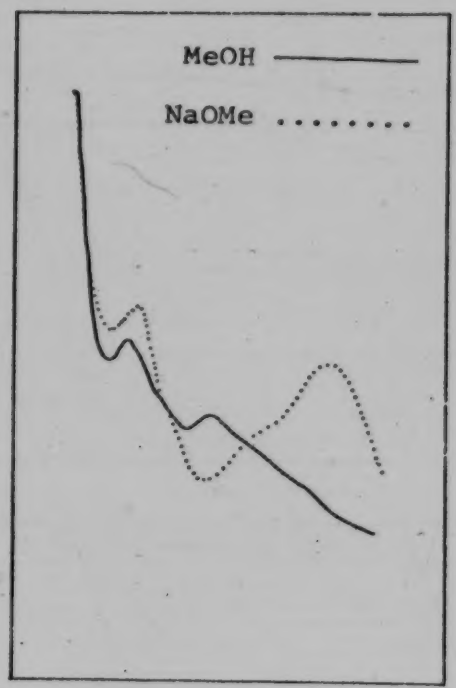


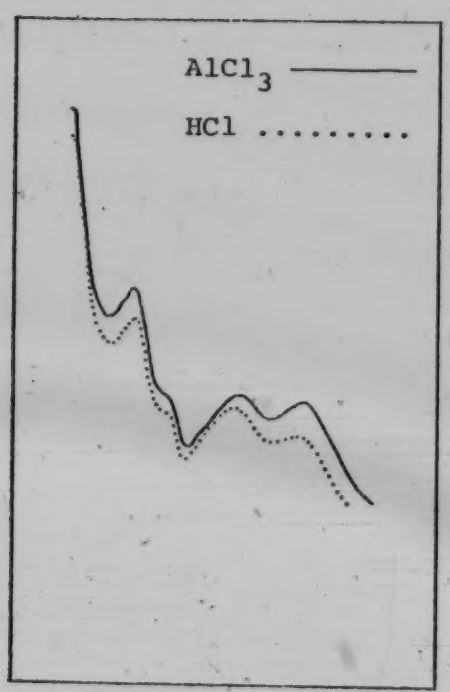
Chromatographic Data

Rf Values				Spot Colour	
BAW	H_2O	HoAc	PhOH	UV	UV/NH_3
29	35	59	71	ppl	ylw

UV Spectral Data

MeOh	272, 330
NaOMe	278, 400
$AlCl_3$	276, 304sh, 354, 400
$AlCl_3$/HCl	276, 304sh, 350, 400
NaOAc	268, 358
H_3BO_3	268, 336





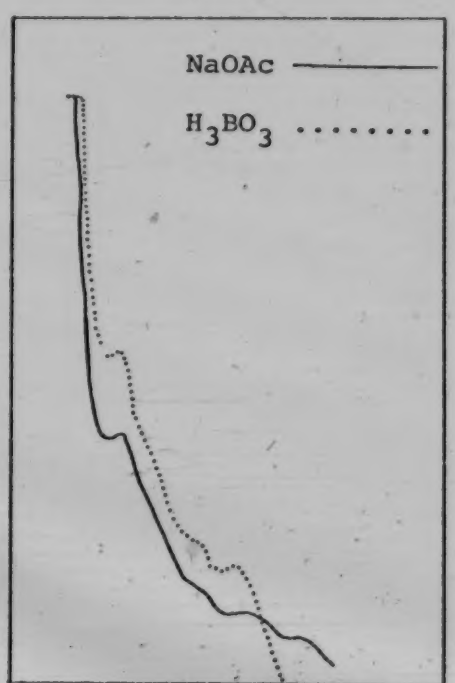
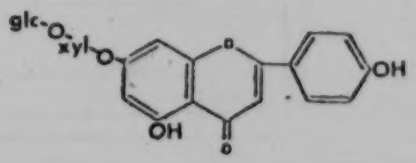
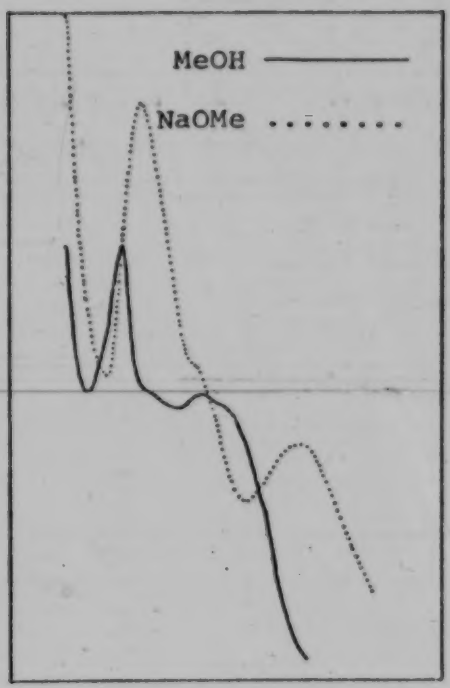


FIGURE 14.

Chromatographic and spectral data for Apigenin 7-O-sambubioside

#5 Apigenin 7-O-sambubioside





Chromatographic Data

Rf Values				Spot Colour	
BAW	H_2O	HoAc	PhOH	UV	UV/NH_3
41	29	61	79	ppl	ylw

UV Spectral Data

MeOH	272, 326
NaOMe	284, 326sh, 398
$AlCl_3$	274, 294sh, 344, 398
$AlCl_3$/HCl	280, 294sh, 346, 398
NaOAc	272, 326
H_3BO_3	270, 348

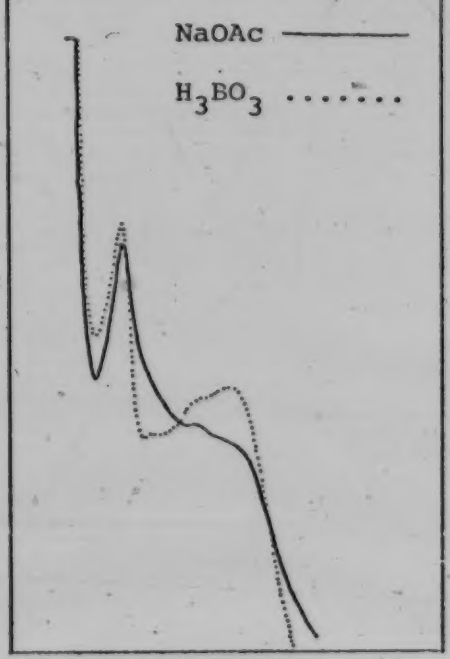
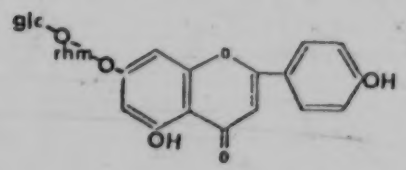


FIGURE 15.

Chromatographic and spectral data for Apigenin 7-O-rutinoside

#6 Apigenin 7-O-rutinoside

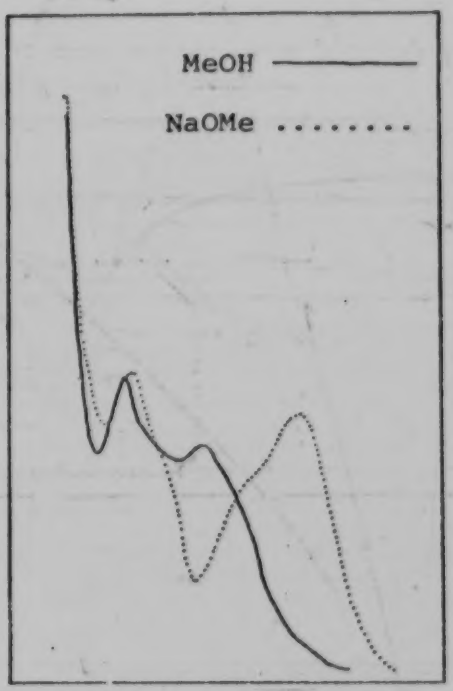


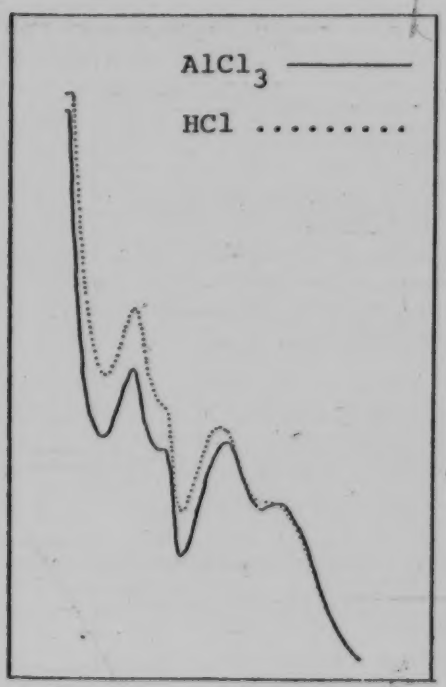
Chromatographic Data

BAW	Rf Values H_2O	HoAc	PhOH	Spot Colour UV	UV/NH_3
62	03	23	81	ppl	yg

UV Spectral Data

MeOh	272, 326
NaOMe	278, 354sh, 396
$AlCl_3$	278, 302sh, 346, 386
$AlCl_3$/HCl	278, 302sh, 340, 386
NaOAc	272, 370
H_3BO_3	270, 334





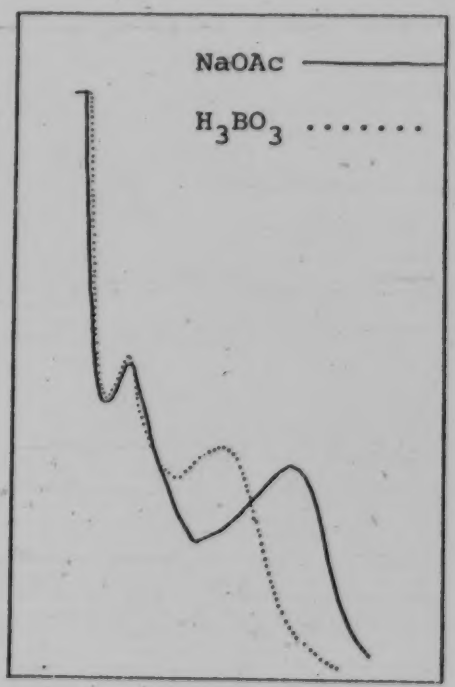
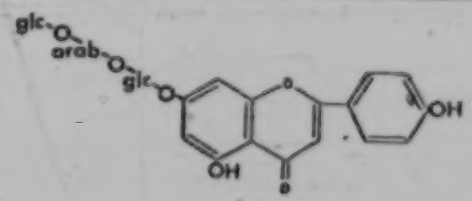
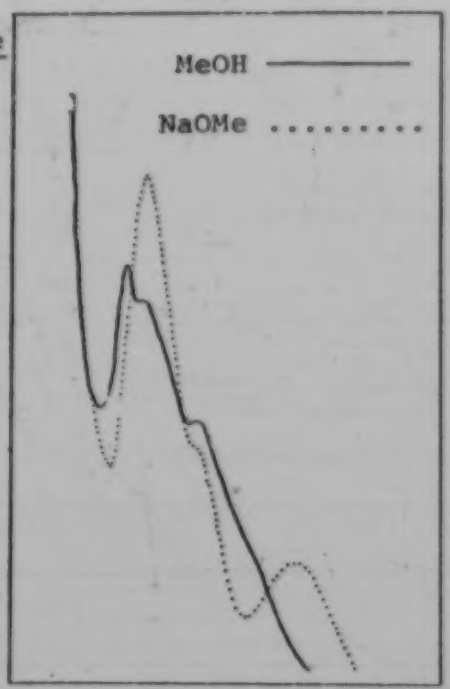


FIGURE 16.

Chromatographic and spectral data for Apigenin 7-O-glucosylvicianoside

#7 Apigenin 7-O-glucosylvicianoside



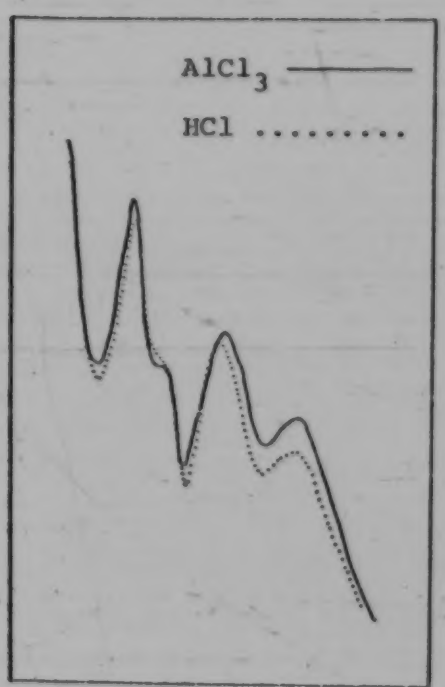


Chromatographic Data

Rf Values				Spot Colour	
BAW	H_2O	HoAc	PhOH	UV	UV/NH_3
45	28	63	74	ppl	yg

UV Spectral Data

MeOH	272, 284, 324
NaOMe	286, 316sh, 394
$AlCl_3$	278, 302sh, 346, 399
$AlCl_3$/HCl	278, 302sh, 346, 398
NaOAc	272, 326
H_3BO_3	270, 324



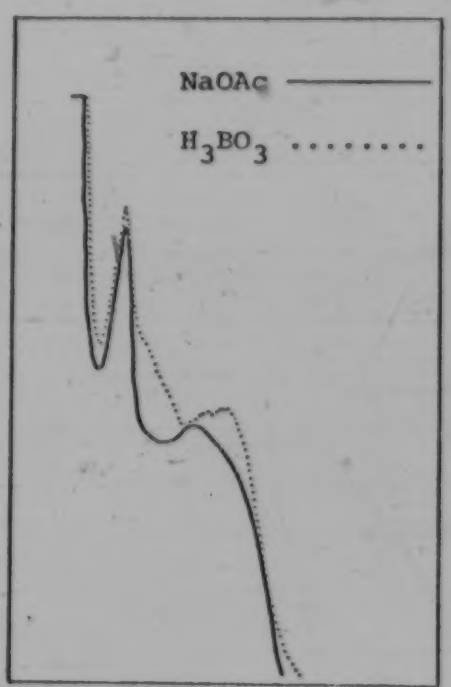
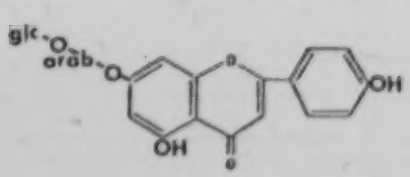
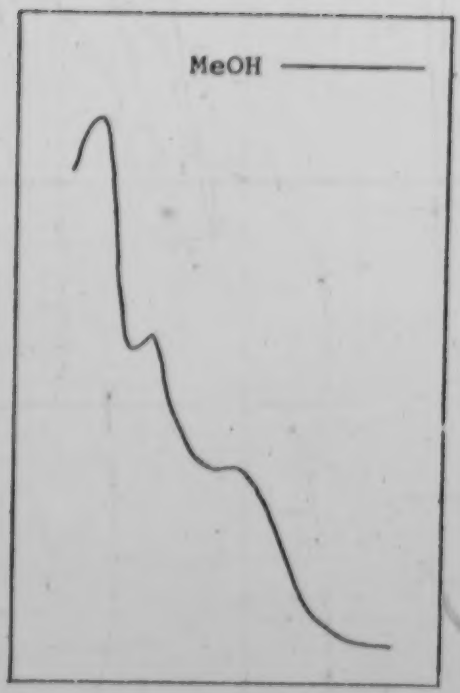


FIGURE 17.

Chromatographic and spectral data for Apigenin 7-O-vicianoside

#8 Apigenin 7-O-vicianoside





Chromatographic Data

	Rf Values			Spot Colour	
BAW	H_2O	HoAc	PhOH	UV	UV/NH_3
54	02	15	83	ppl	yg

UV Spectral Data

MeOh	268, 330
NaOMe	
$AlCl_3$	274, 302sh, 340, 383
$AlCl_3$/HCl	274, 302sh, 340, 380
NaOAc	
H_3BO_3	

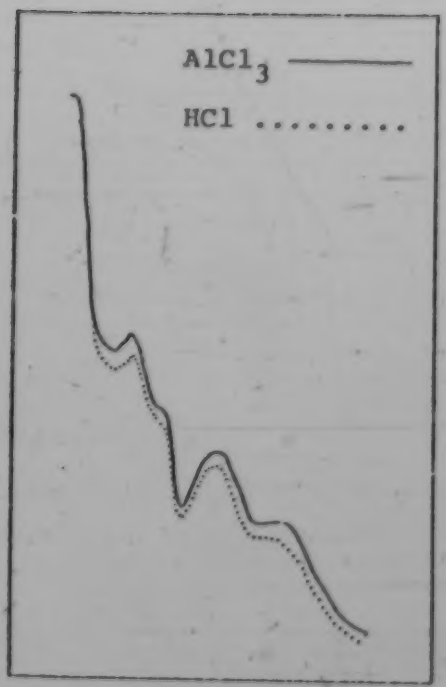
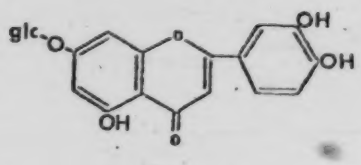


FIGURE 18.

Chromatographic and spectral data for Luteolin 7-O-glucoside

#9 Luteolin 7-O-glucoside

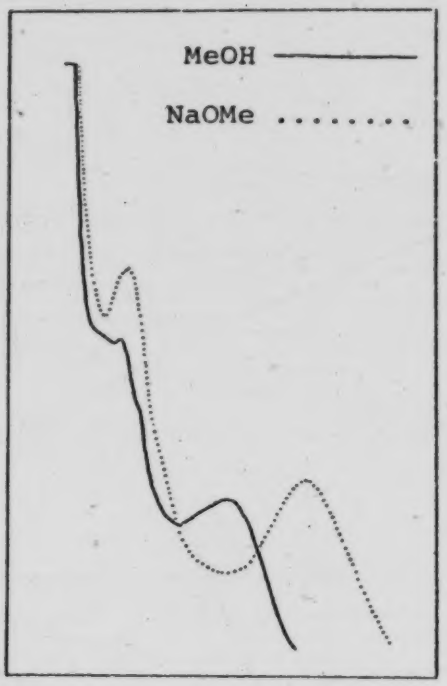


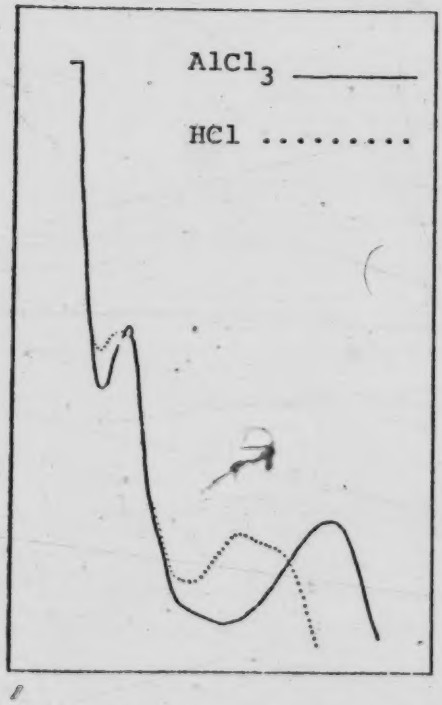
Chromatographic Data

	Rf Values			Spot Colour	
BAW	H_2O	HoAc	PhOH	UV	UV/NH_3
47	02	11	56 38	ppl	ylw

UV Spectral Data

MeOH	256, 270sh, 346
NaOMe	274, 402
$AlCl_3$	276, 425
$AlCl_3$/HCl	270, 358
NaOAc	268, 376
H_3BO_3	260, 370





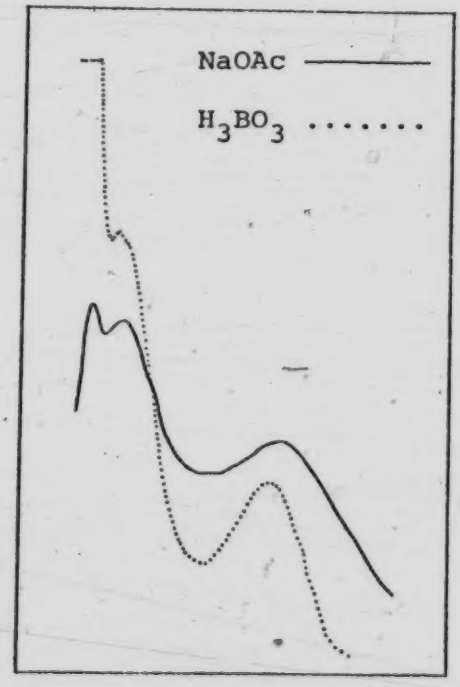
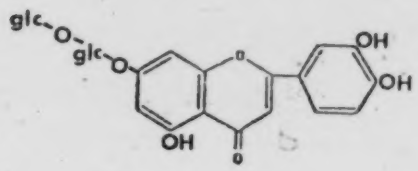


FIGURE 19.

Chromatographic and spectral data for Luteolin 7-O-diglucoside

#10 Luteolin 7-O-diglucoside

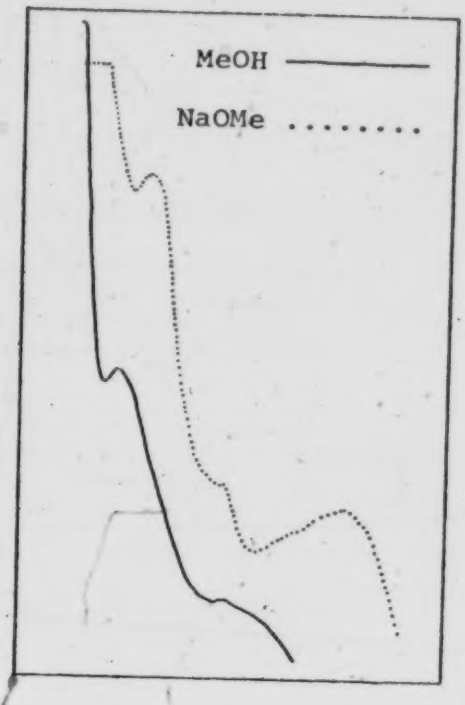


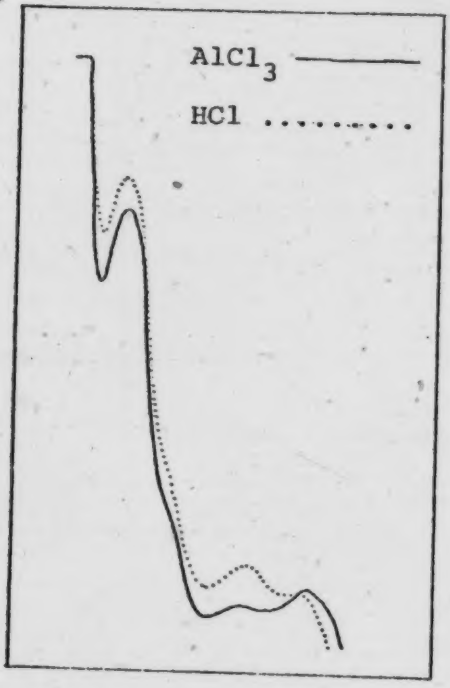
Chromatographic Data

Rf Values				Spot Colour	
BAW	H_2O	HOAc	PhOH	UV	UV/NH_3
48	25	48	66	ppl	ylw

UV Spectral Data

MeOh	258, 270sh, 334
NaOMe	282, 330sh, 428
$AlCl_3$	270, 360, 406
$AlCl_3$/HCl	268, 360
NaOAc	270, 406
H_3BO_3	258, 360





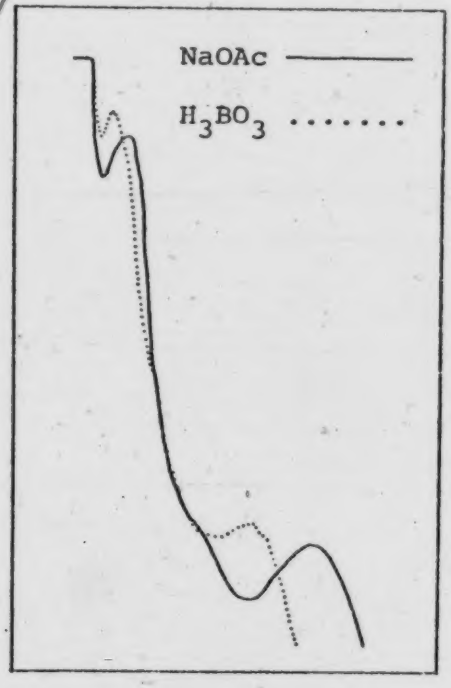
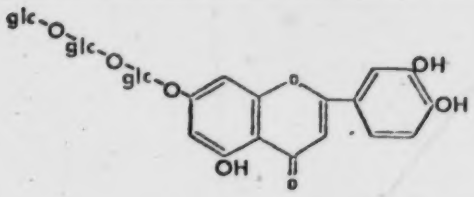


FIGURE 20.

Chromatographic and spectral data for Luteolin 7-O-triglucoside

#11 Luteolin 7-O-triglucoside

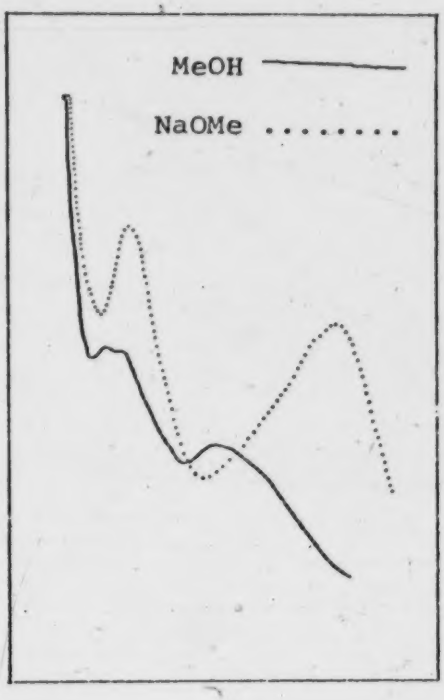


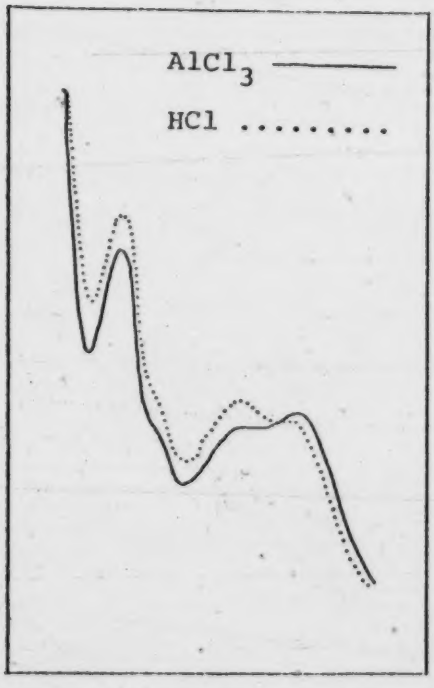
Chromatographic Data

	Rf Values			Spot Colour	
BAW	H_2O	HoAc	PhOH	UV	UV/NH_3
28	31	68	47	ppl	yg

UV Spectral Data

MeOH	258, 268sh, 338
NaOMe	274, 422
$AlCl_3$	272, 306sh, 398
$AlCl_3$/HCl	274, 360
NaOAc	268, 406
H_3BO_3	258, 358





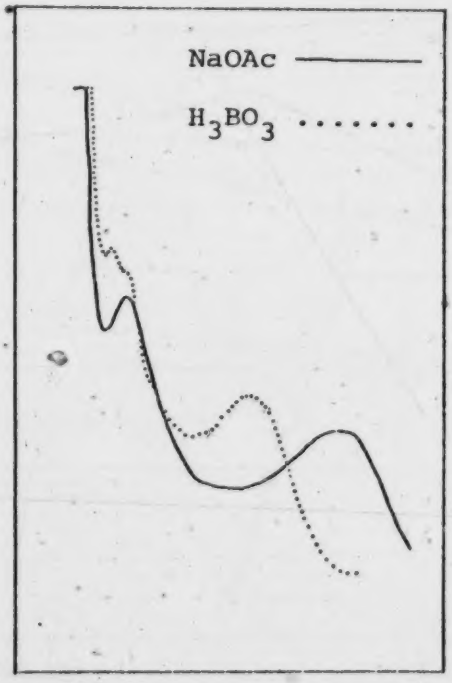
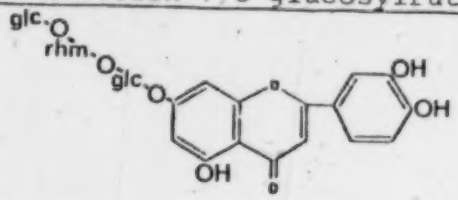


FIGURE 21.

Chromatographic and spectral data for Luteolin 7-O-glucosylrutinoside

#12 Luteolin 7-O-glucosylrutinoside

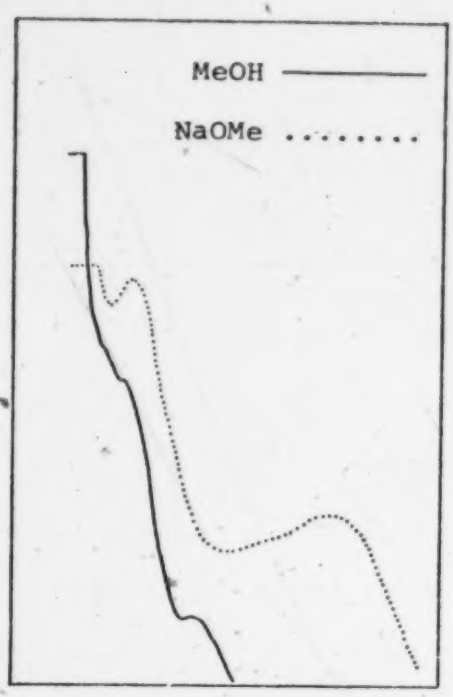


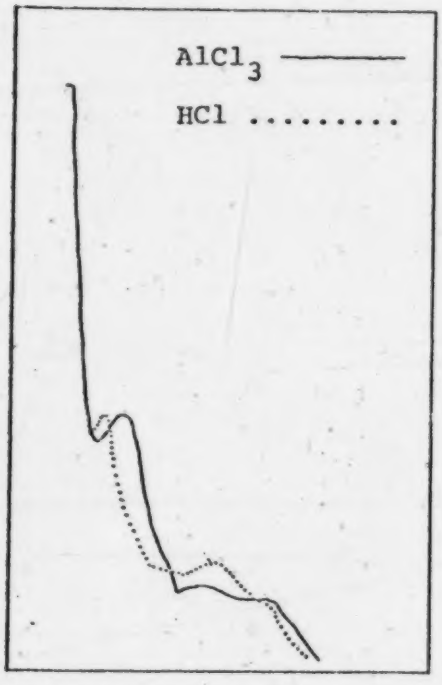
Chromatographic Data

Rf Values				Spot Colour	
BAW	H_2O	HoAc	PhOH	UV	UV/NH_3
30	29	62	61	ppl	yg

UV Spectral Data

MeOh	258, 268sh, 330
NaOMe	274, 404, 428
$AlCl_3$	272, 350, 400
$AlCl_3$/HCl	273, 358
NaOAc	258, 400
H_3BO_3	258, 360





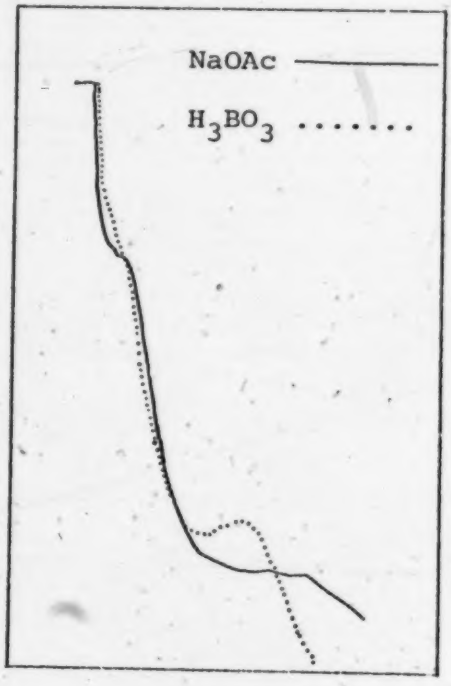
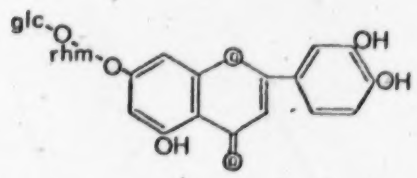


FIGURE 22.

Chromatographic and spectral data for Luteolin 7-O-rutinoside

#13 Luteolin 7-O-rutinoside

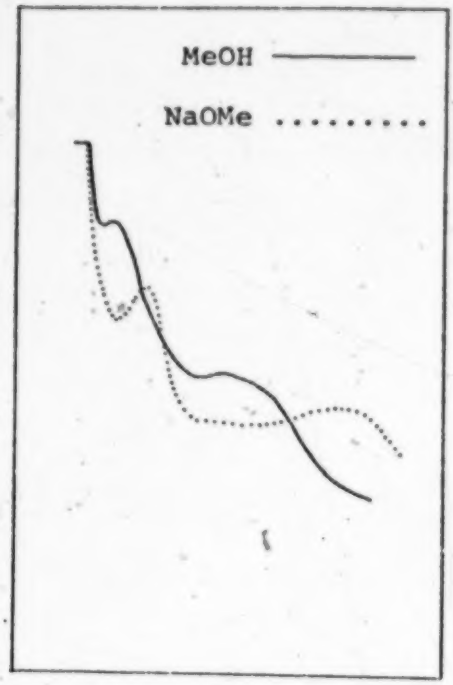


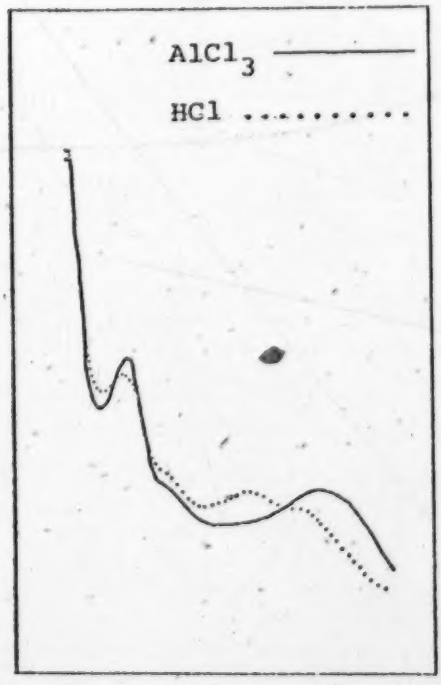
Chromatographic Data

Rf Values				Spot Colour	
BAW	H_2O	HoAc	PhOH	UV	UV/NH_3
51	52	39	25	ppl	yg

UV Spectral Data

MeOH	258, 268sh, 334
NaOMe	282, 418
$AlCl_3$	274, 306sh, 414
$AlCl_3$/HCl	270, 306sh, 362
NaOAc	272, 380
H_3BO_3	262, 370





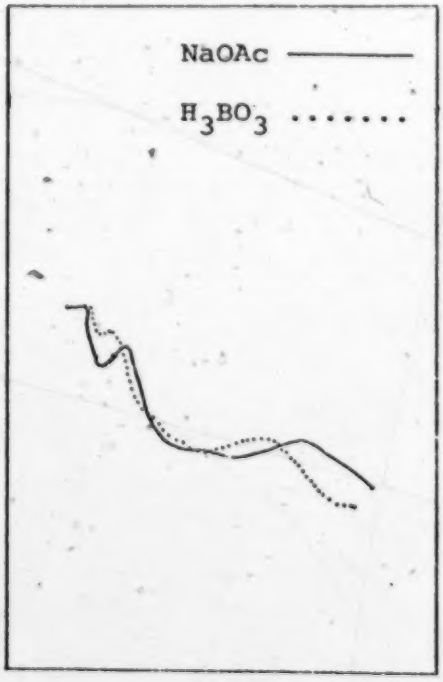
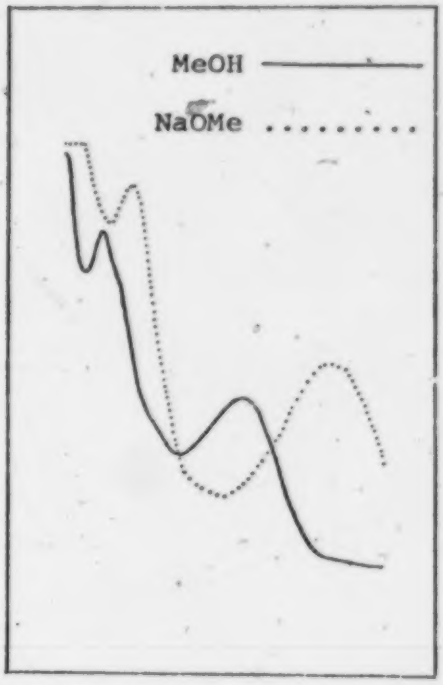


FIGURE 23.

Chromatographic and spectral data for glycoside #14

#14

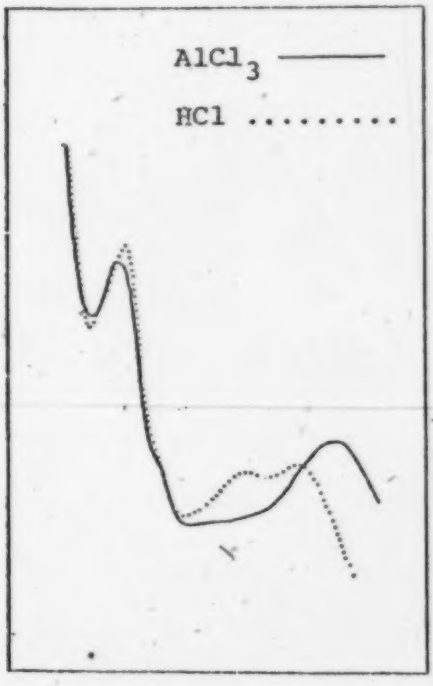


Chromatographic Data

Rf Values				Spot Colour	
BAW	H_2O	HoAc	PhOH	UV	UV/NH_3
36	38	61	47	ppl	ylw

UV Spectral Data

MeOh	276, 286sh, 344
NaOMe	280, 286sh, 414
$AlCl_3$	280, 346, 398
$AlCl_3$/HCl	280, 350, 398
NaOAc	272, 386
H_3BO_3	274, 362



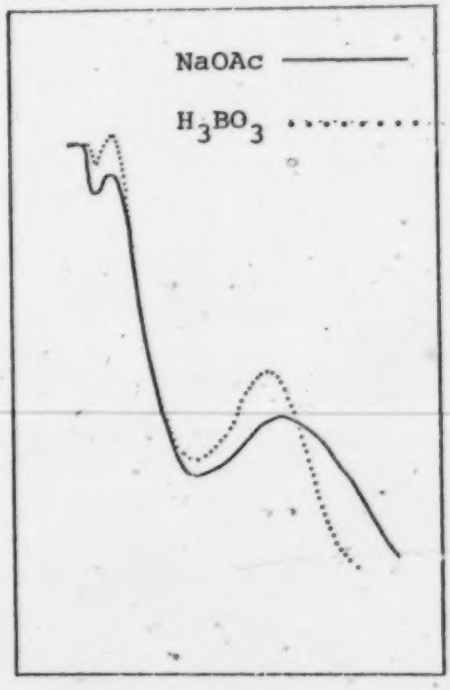
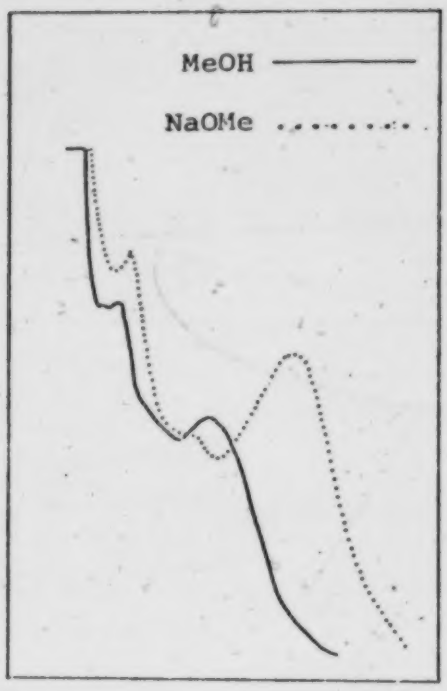


FIGURE 24.

Chromatographic and spectral data for glycoside #15'

#15

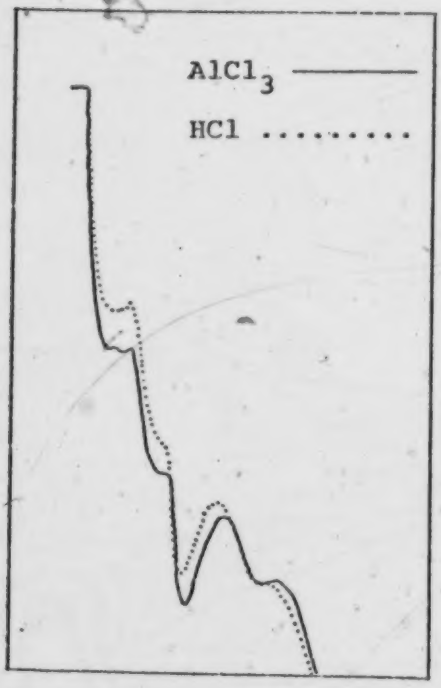


Chromatographic Data

Rf Values				Spot Colour	
BAW	H_2O	HoAc	PhOH	UV	UV/NH_3
89	02	04	55	ppl	ylw

UV Spectral Data

MeOH	258, 268sh, 330
NaOMe	278, 312, 396
$AlCl_3$	276, 304sh, 346, 386
$AlCl_3$/HCl	276, 304sh, 342
NaOAc	266, 384
H_3BO_3	266, 330



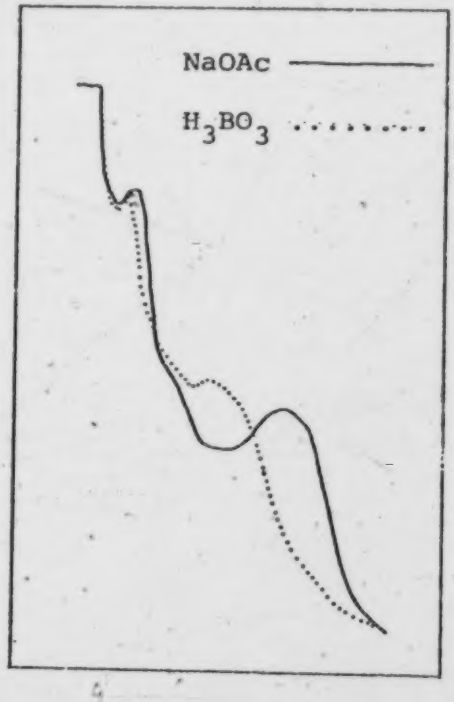
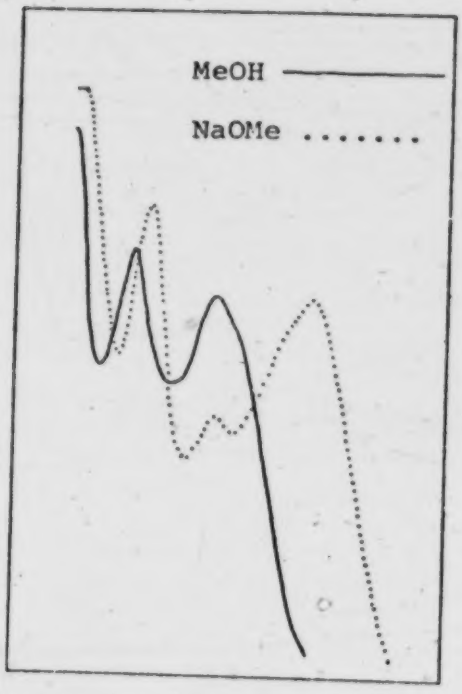


FIGURE 25.

Chromatographic and spectral data for glycoside #16

#16



Chromatographic Data

	Rf Values			Spot Colour	
BAW	H_2O	HoAc	PhOH	UV	UV/NH_3
26	69	53	58	ppl	yg

UV Spectral Data

MeOh	274, 338
NaOMe	286, 332, 402
$AlCl_3$	282, 306, 350, 388
$AlCl_3$/HCl	282, 306, 348
NaOAc	284, 398
H_3BO_3	278, 350

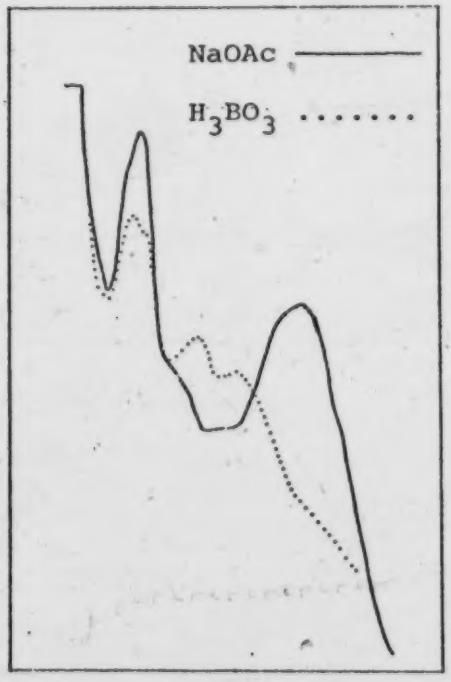
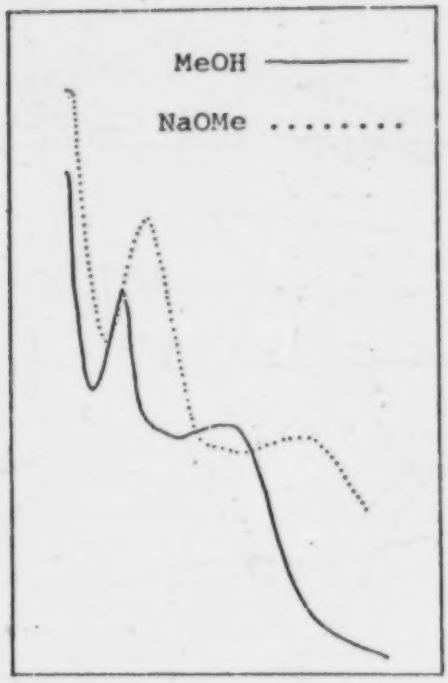


FIGURE 26.

Chromatographic and spectral data for glycoside #17

#17

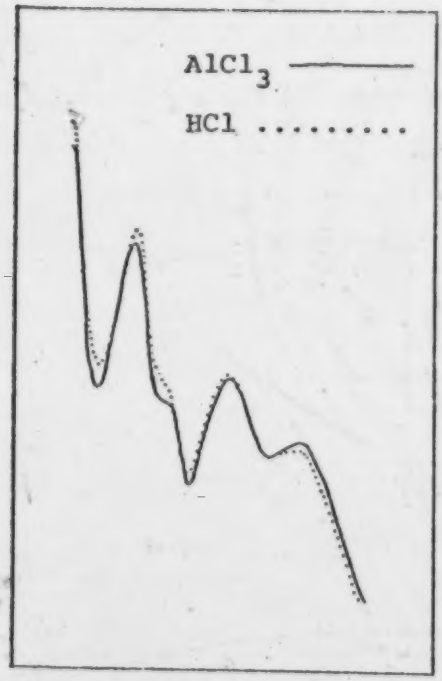


Chromatographic Data

Rf Values				Spot Colour	
BAW	H_2O	HoAc	PhOH	UV	UV/NH_3
33	33	71	54	ppl	yg

UV Spectral Data

MeOH	270, 340
NaOMe	286, 402
$AlCl_3$	278, 346, 401
$AlCl_3$/HCl	278, 346, 401
NaOAc	274, 350
H_3BO_3	274, 350



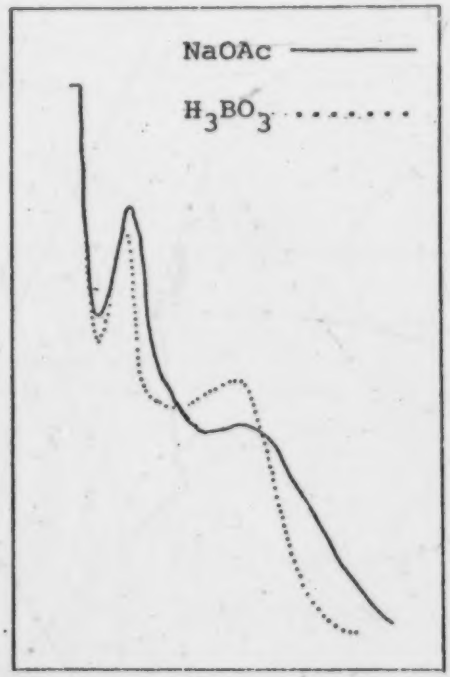
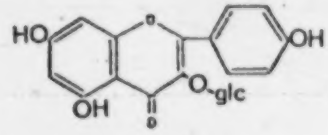
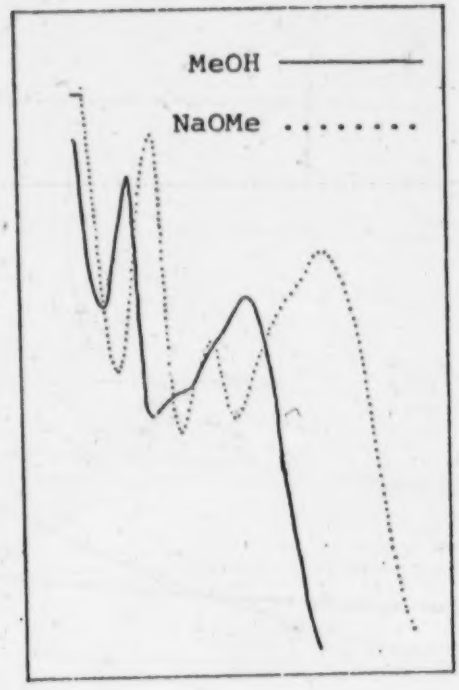


FIGURE 27.

Chromatographic and spectral data for Kaempferol 3-O-glucoside

#18 Kaempferol 3-O-glucoside





Chromatographic Data

Rf Values				Spot Colour	
BAW	H_2O	HoAc	PhOH	UV	UV/NH_3
76	13	43	68	ppl	yg

UV Spectral Data

MeOh	268, 351
NaOMe	283, 326, 406
$AlCl_3$	276, 306sh, 350, 399
$AlCl_3$/HCl	276, 306sh, 350, 399
NaOAc	238, 274, 308, 378
H_3BO_3	270, 301, 356

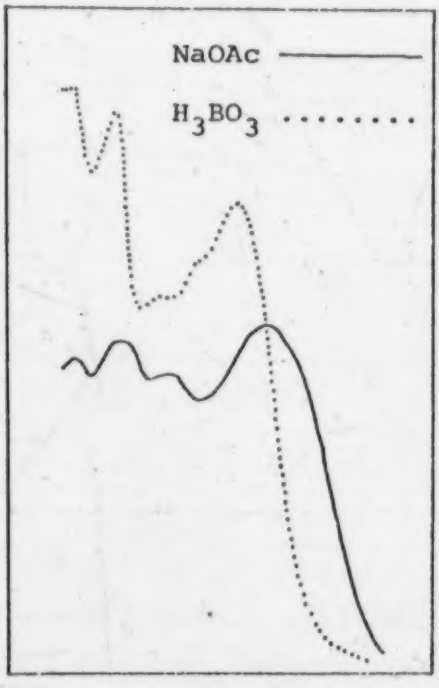
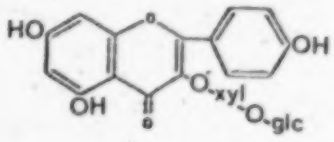
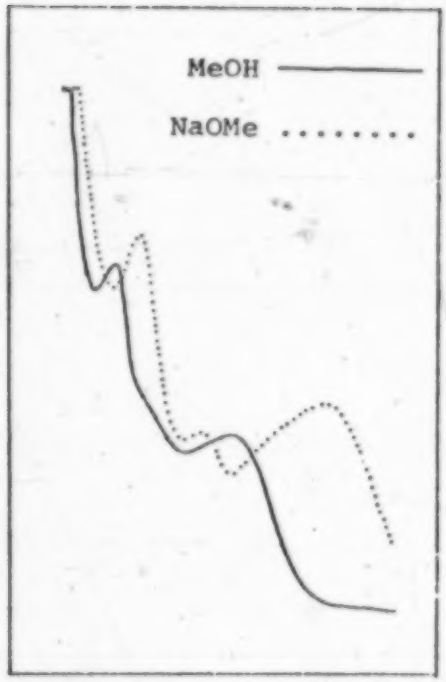


FIGURE 28.

Chromatographic and spectral data for Kaempferol 3-O-sambubioside

#19 Kaempferol 3-O-sambubioside



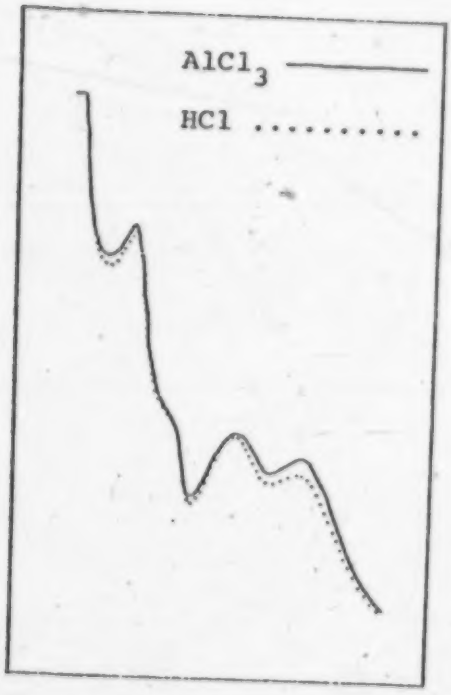


Chromatographic Data

Rf Values				Spot Colour	
BAW	H_2O	HoAc	PhOH	UV	UV/NH_3
66	23	53	62	ppl	yg

UV Spectral Data

MeOH	267, 350
NaOMe	284,328, 410
$AlCl_3$	275, 306sh, 352, 400
$AlCl_3$/HCl	275, 306sh, 352, 400
NaOAc	275, 378
H_3BO_3	268, 354



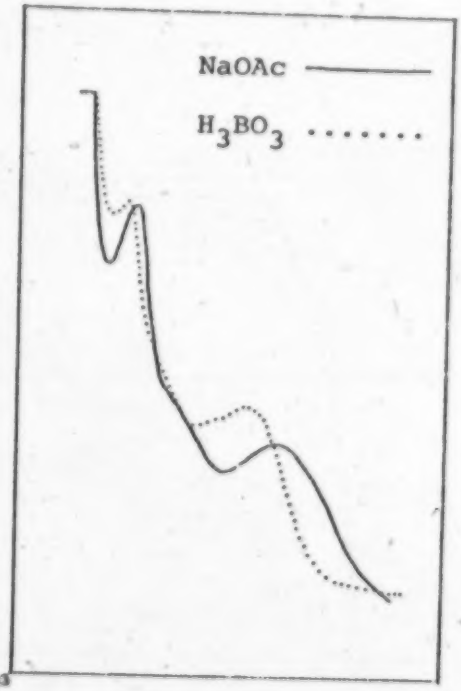
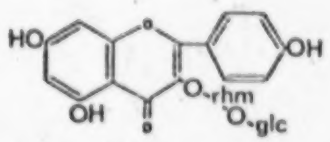


FIGURE 29.

Chromatographic and spectral data for Kaempferol 3-O-rutinoside

#20 Kaempferol 3-O-rutinoside

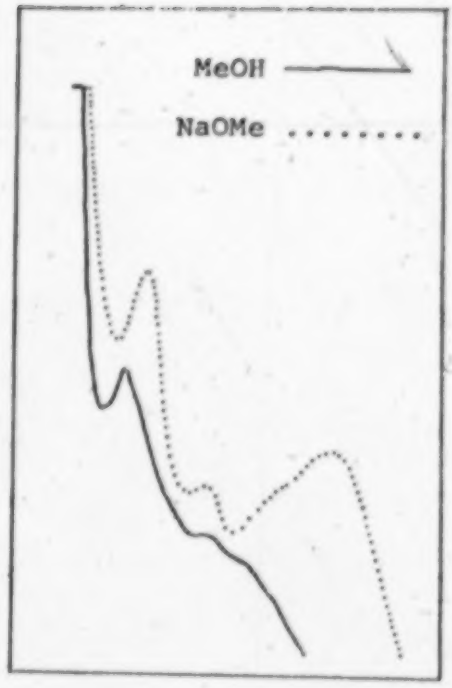


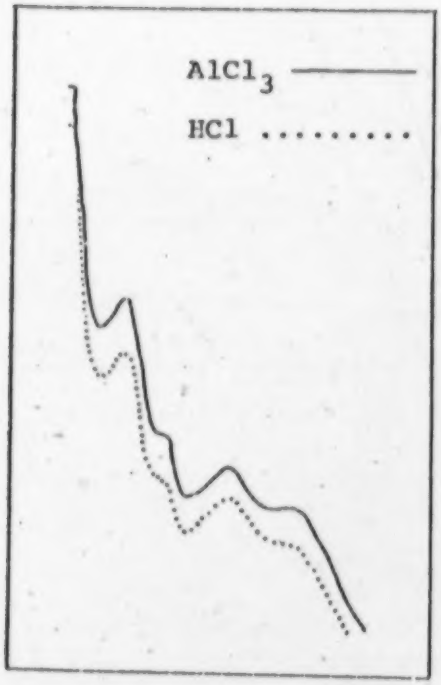
Chromatographic Data

Rf Values				Spot Colour	
BAW	H_2O	HoAc	PhOH	UV	UV/NH_3
58	54	54	61	ppl	yg

UV Spectral Data

MeOh	268, 350
NaOMe	284, 326, 418
$AlCl_3$	274, 306sh, 348, 398
$AlCl_3$/HCl	274, 306sh, 348, 398
NaOAc	276, 388
H_3BO_3	268, 350





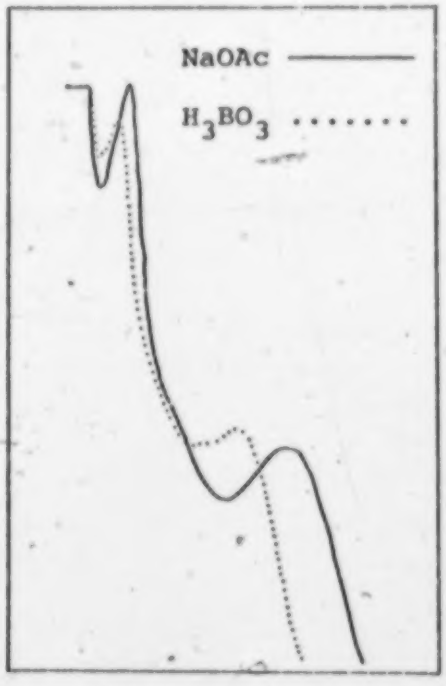
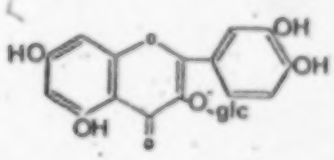
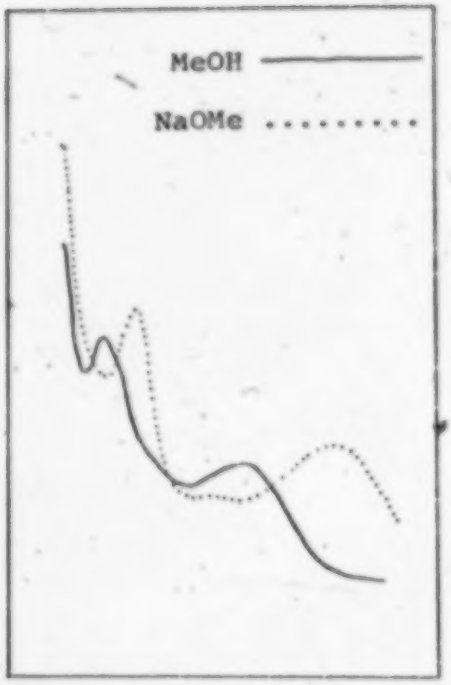


FIGURE 30.

Chromatographic and spectral data for Quercetin 3-O-glucoside

#21 Quercetin 3-O-glucoside isomer #1



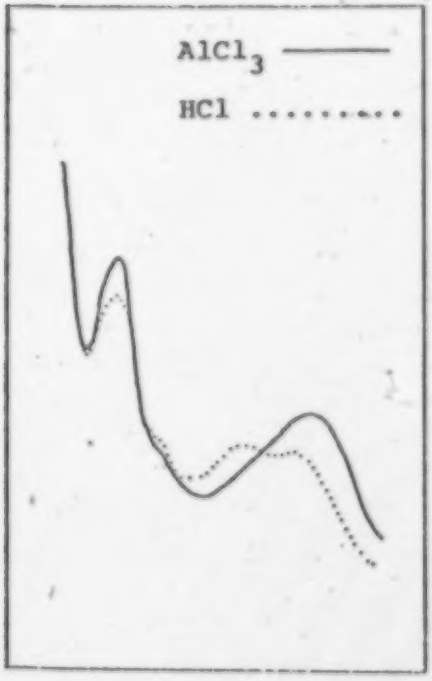


Chromatographic Data

Rf Values				Spot Colour	
BAW	H_2O	HoAc	PhOH	UV	UV/NH_3
58	06	34	29	ppl	ylw

UV Spectral Data

MeOH	257, 268sh, 358
NaOMe	280, 334, 424
$AlCl_3$	272, 412
$AlCl_3$/HCl	270, 364
NaOAc	274, 408
H_3BO_3	262, 374



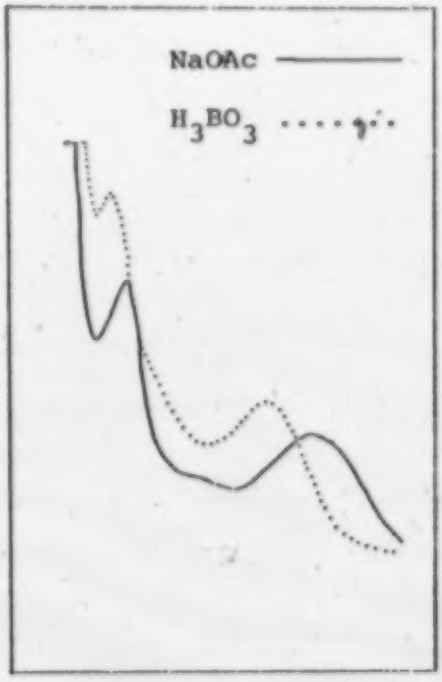
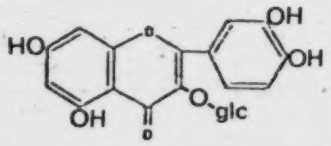


FIGURE 31.

Chromatographic and spectral data for Quercetin 3-O-glucoside

#22 Quercetin 3-O-glucoside
isomer #2

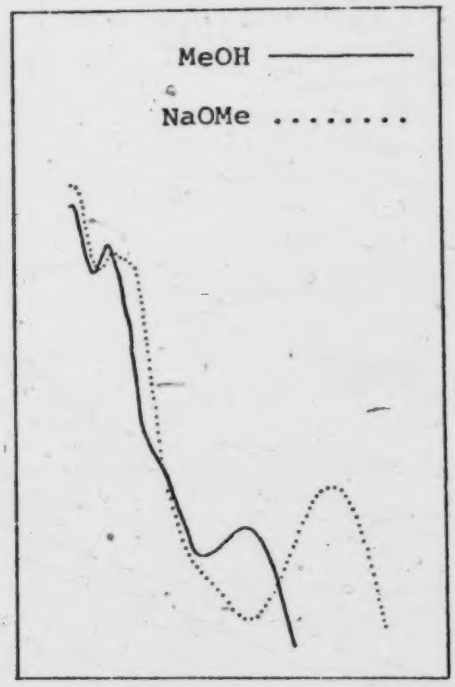


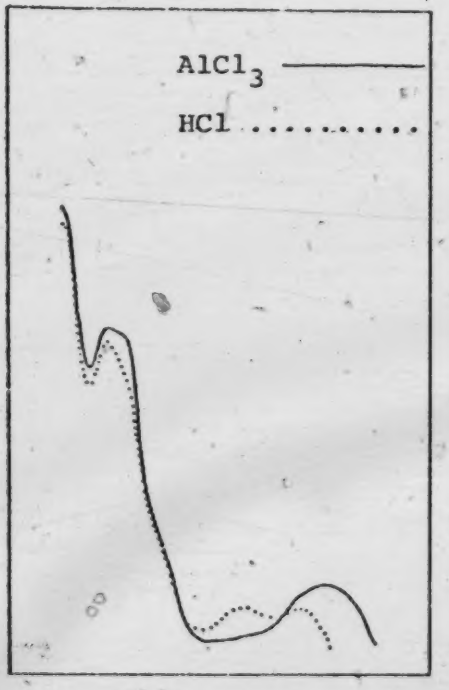
Chromatographic Data

	Rf Values			Spot Colour	
BAW	H_2O	HOAc	PhOH	UV	UV/NH_3
57	14	32	75 51	ppl	ylw

UV Spectral Data

MeOh	258, 268sh, 354
NaOMe	260, 276sh, 414
$AlCl_3$	262, 276sh, 420
$AlCl_3$/HCl	262, 360
NaOAc	272, 398
H_3BO_3	258, 368





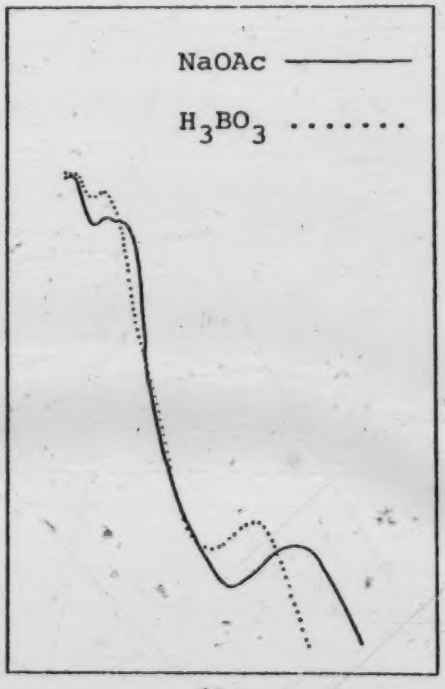
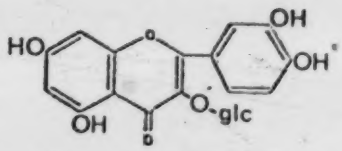


FIGURE 32.

Chromatographic and spectral data for Quercetin 3-O-glucoside

#23 Quercetin 3-O-glucoside

isomer #3

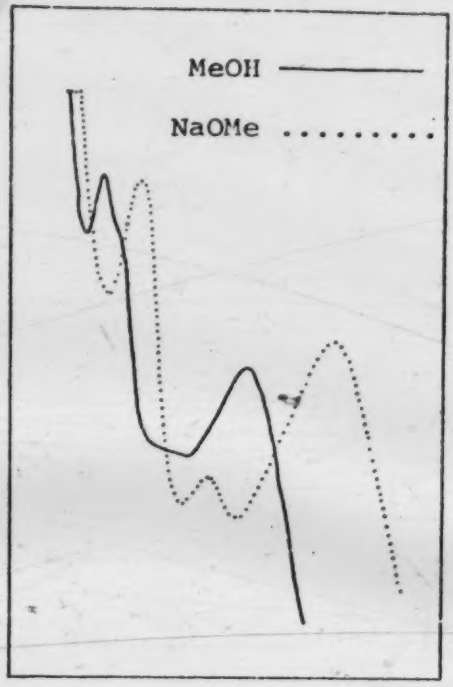


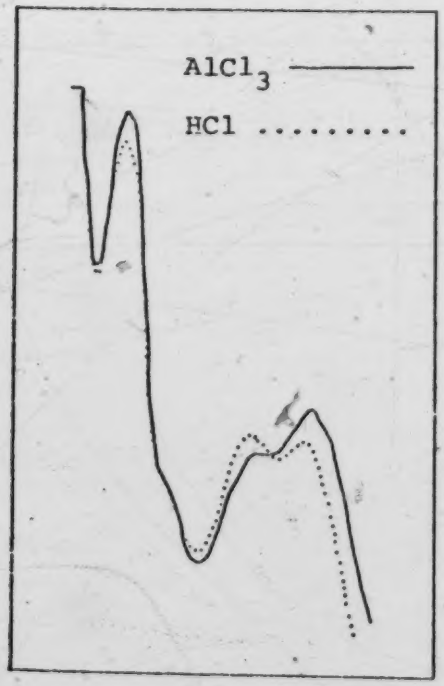
Chromatographic Data

Rf Values				Spot Colour	
BAW	H_2O	HoAc	PhOH	UV	UV/NH_3
70	09	38	70	ppl	ylw
			41		

UV Spectral Data

MeOH	256, 268sh, 358
NaOMe	282, 332, 418
$AlCl_3$	270, 306sh, 370, 406
$AlCl_3$/HCl	268, 306sh, 362
NaOAc	238, 273, 320, 400
H_3BO_3	---, 362





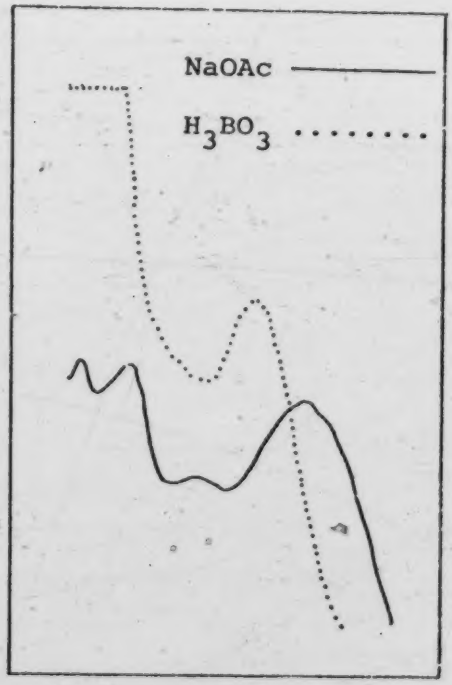
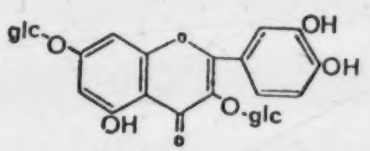
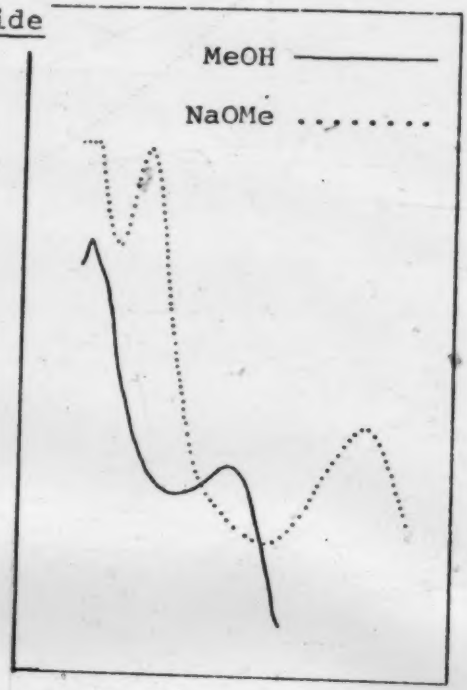


FIGURE 33.

Chromatographic and spectral data for Quercetin 3-O-glucose-7-O-glucoside

#24 Quercetin 3-O-glucose-7-O-glucoside



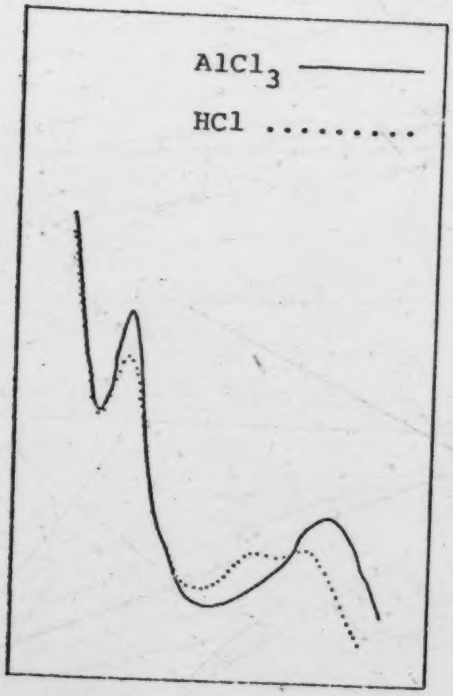


Chromatographic Data

Rf Values				Spot Colour	
BAW	H_2O	HoAc	PhOH	UV	UV/NH_3
19	30	62	28	ppl	ylw

UV Spectral Data

MeOh	258, 268sh, 358
NaOMe	276, 430
$AlCl_3$	274, 420
$AlCl_3$/HCl	272, 366
NaOAc	270, 402
H_3BO_3	262, 378



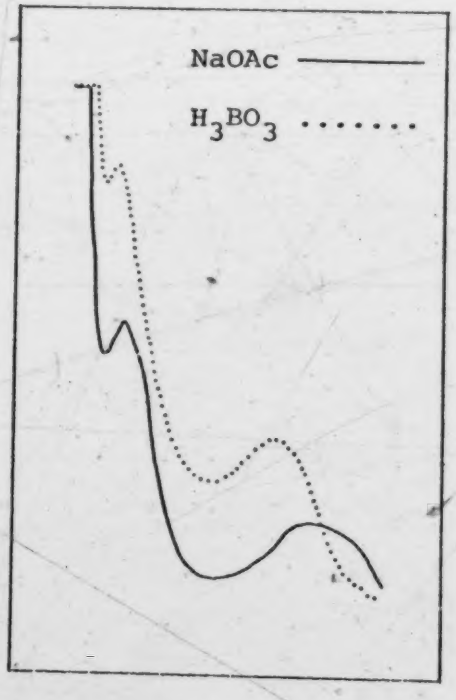
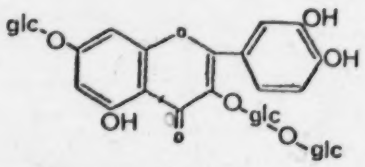
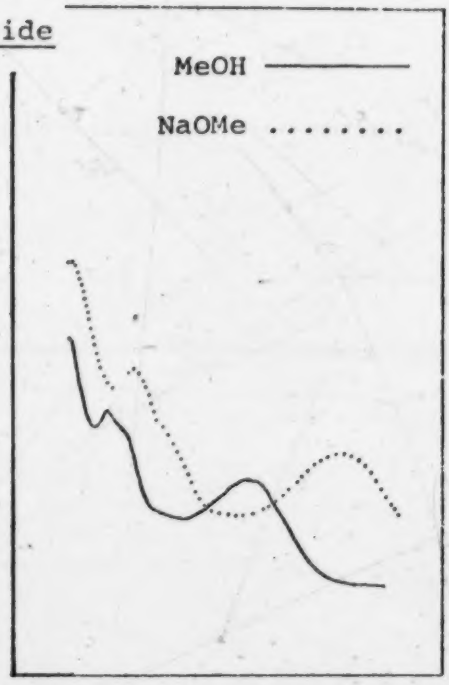


FIGURE 34.

Chromatographic and spectral data for Quercetin 3-O-sophoroside-7-O-glucoside

#25 Quercetin 3-O-sophoroside-7-O-glucoside



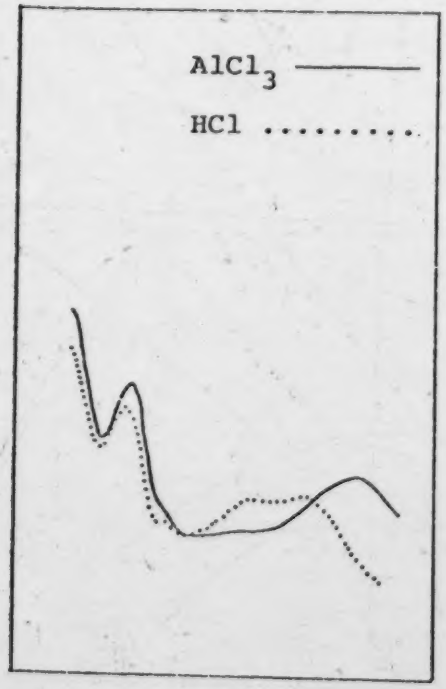


Chromatographic Data

	Rf Values			Spot Colour	
BAW	H_2O	HoAc	PhOH	UV	UV/NH_3
10	59	74	34	ppl	ylw

UV Spectral Data

MeOH	258, 270sh, 358
NaOMe	276, 422
$AlCl_3$	276, 438
$AlCl_3$/HCl	270, 366
NaOAc	266, 384
H_3BO_3	264, 378



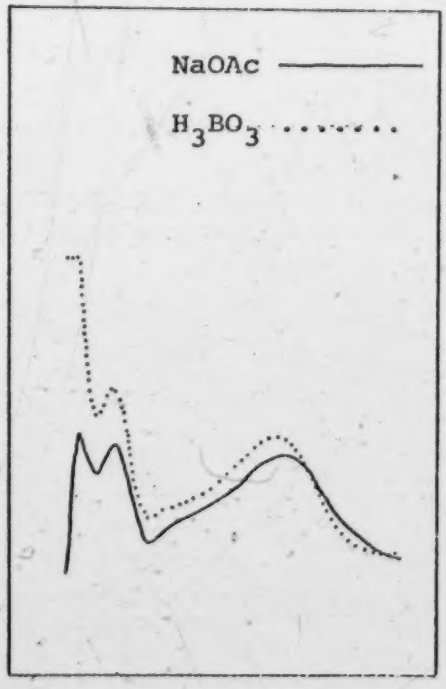
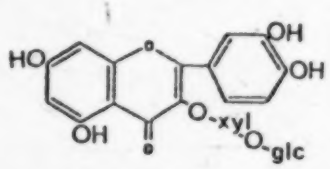


FIGURE 35.

Chromatographic and spectral data for Quercetin 3-O-sambubioside

#26 Quercetin 3-O-sambubioside

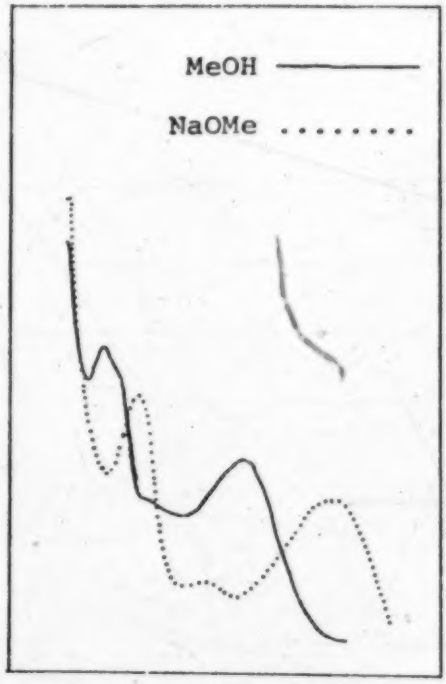


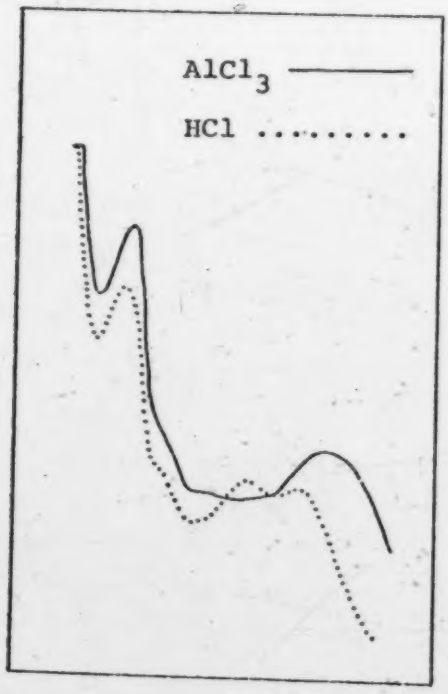
Chromatographic Data

	Rf Values			Spot Colour	
BAW	H_2O	HoAc	PhOH	UV	UV/NH_3
58	18	48	67 48	ppl	yg

UV Spectral Data

MeOh	258, 270sh, 358
NaOMe	282, 330, 420
$AlCl_3$	276, 305sh, 420
$AlCl_3$/HCl	270, 306sh, 362
NaOAc	276, 402
H_3BO_3	260, 370





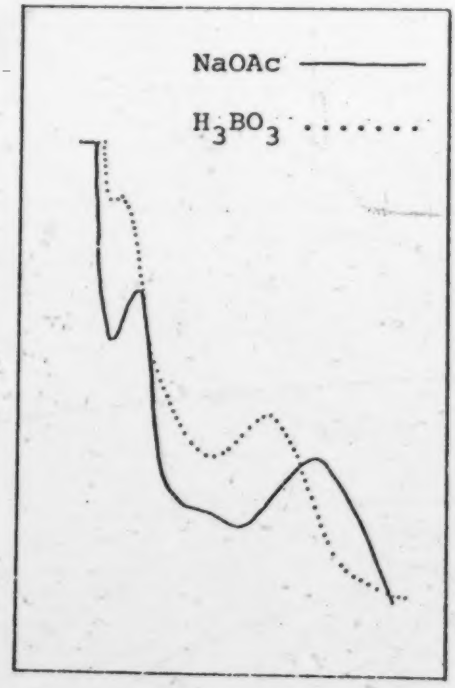
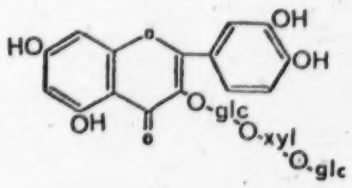
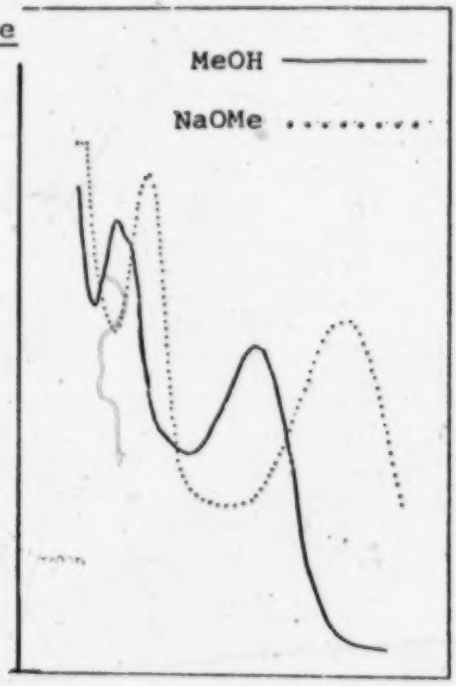


FIGURE 36.

Chromatographic and spectral data for Quercetin 3-O-diglucosylxyloside

#27 Quercetin 3-O-diglucosylxyloside





Chromatographic Data

	Rf Values			Spot Colour	
BAW	H_2O	HoAc	PhOH	UV	UV/NH_3
54	26	60	53	ppl	yg

UV Spectral Data

MeOH	258, 270sh, 358
NaOMe	281, 422
$AlCl_3$	272, 306sh, 424
$AlCl_3$/HCl	272, 306sh, 362
NaOAc	272, 326, 394
H_3BO_3	264, 292sh, 376

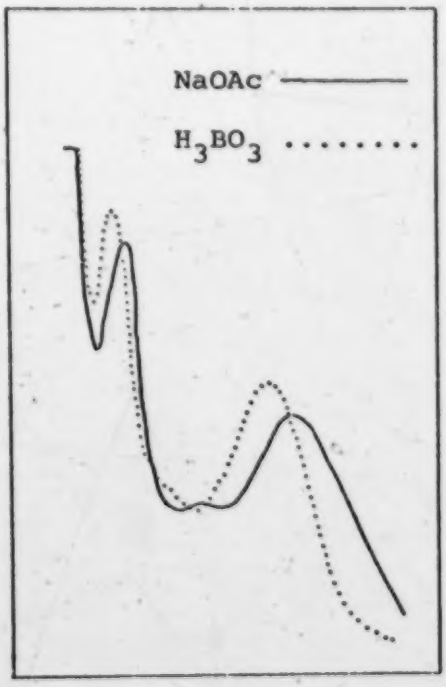
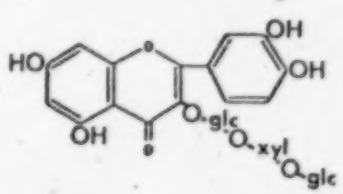


FIGURE 37.

Chromatographic and spectral data for Quercetin 3-O-diglucosylxyloside

#28 Quercetin 3-O-diglucosylxyloside

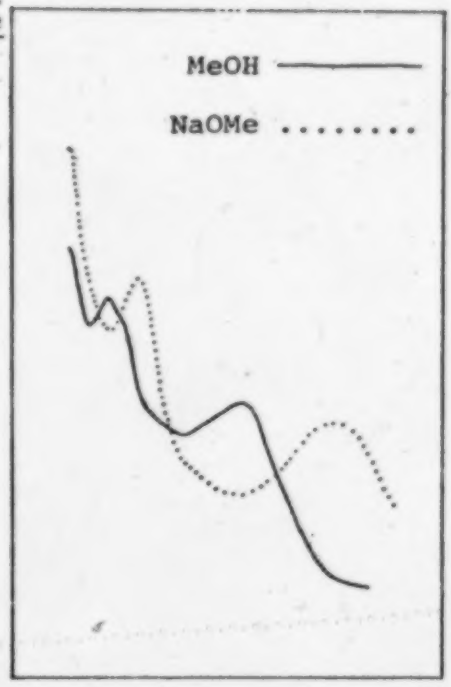


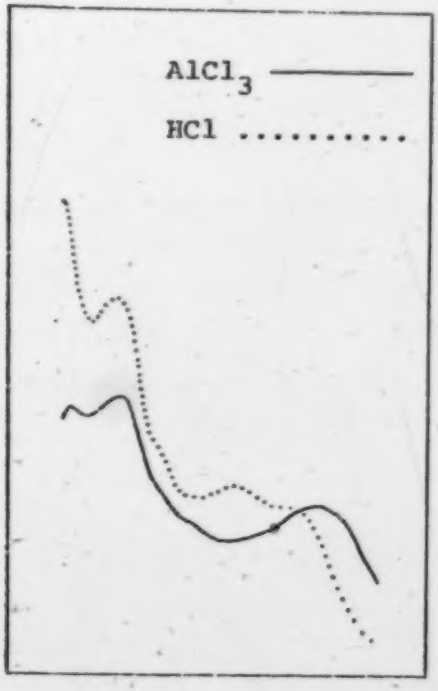
Chromatographic Data

Rf Values				Spot Colour	
BAW	H_2O	HoAc	PhOH	UV	UV/NH_3
44	25	57	25	ppl	yg

UV Spectral Data

MeOh	258, 270sh, 356
NaOMe	280, 418
$AlCl_3$	236, 272, 414
$AlCl_3$/HCl	268, 360
NaOAc	268, 330, 386
H_3BO_3	262, 368





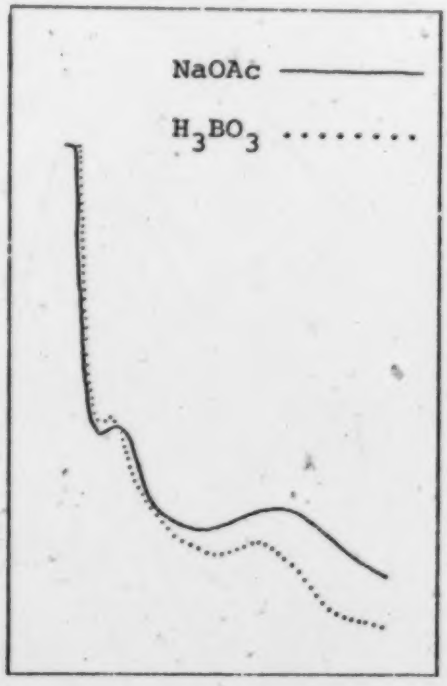
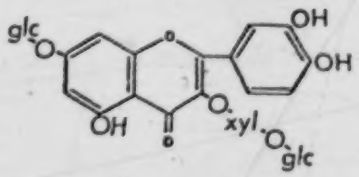


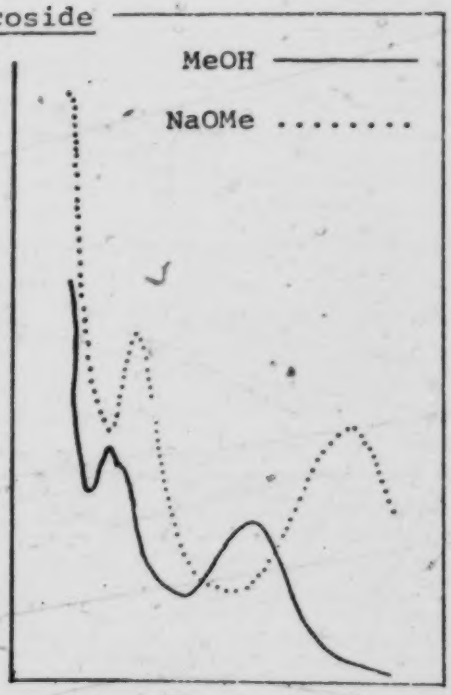
FIGURE 38.

Chromatographic and spectral data for Quercetin

3-O-sambubioside-7-O-glucoside

#29 Quercetin 3-O-sambubioside-7-O-glucoside



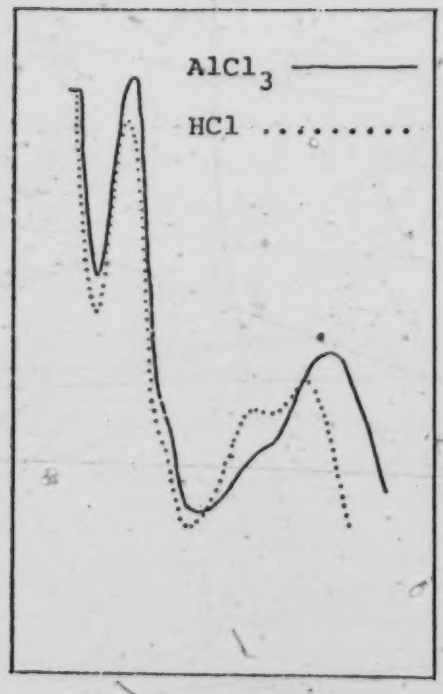


Chromatographic Data

Rf Values				Spot Colour	
BAW	H_2O	HoAc	PhOH	UV	UV/NH_3
27	53	71	46	ppl	ylw

UV Spectral Data

MeOH	260, 270sh, 362
NaOMe	280, 428
$AlCl_3$	274, 418
$AlCl_3$/HCl	272, 366
NaOAc	268, 410
H_3BO_3	264, 380



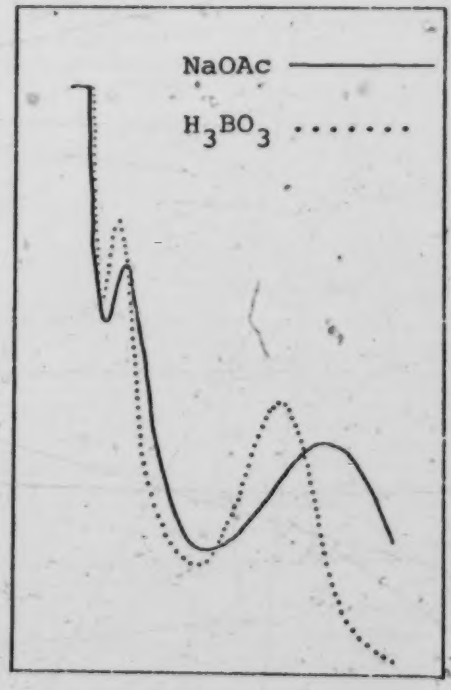
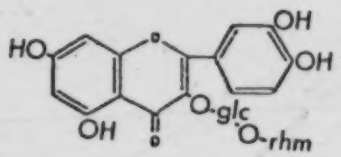
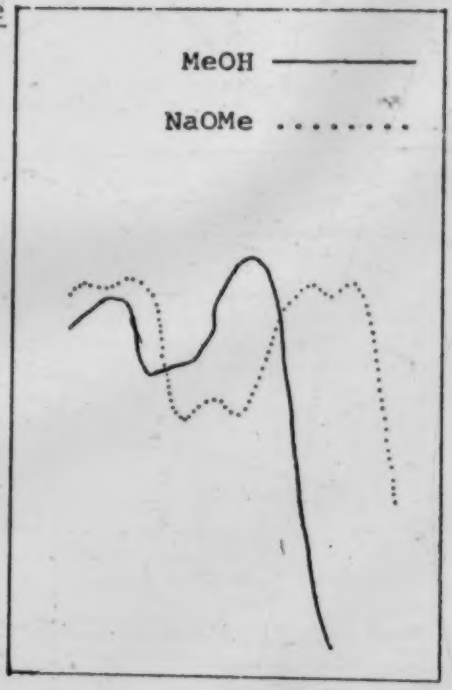


FIGURE 39.

Chromatographic and spectral data for Quercetin 3-O-glucosylrhamnoside

#30 Quercetin 3-O-glucosylrhamnoside



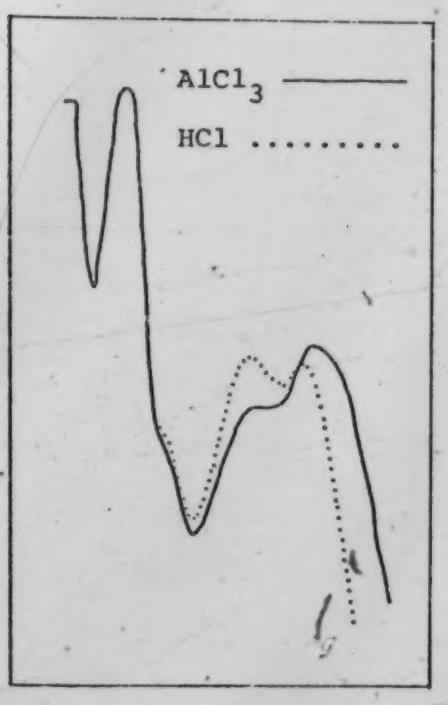


Chromatographic Data

Rf Values				Spot Colour	
BAW	H_2O	HoAc	PhOH	UV	UV/NH_3
63	10	36	69 46	ppl	ylw

UV Spectral Data

MeOh	258, 268sh, 360
NaOMe	276, 332, 404, 430
$AlCl_3$	272, 304sh, 412
$AlCl_3$/HCl	272, 304sh, 362
NaOAc	276, 326, 394
H_3BO_3	262, 370



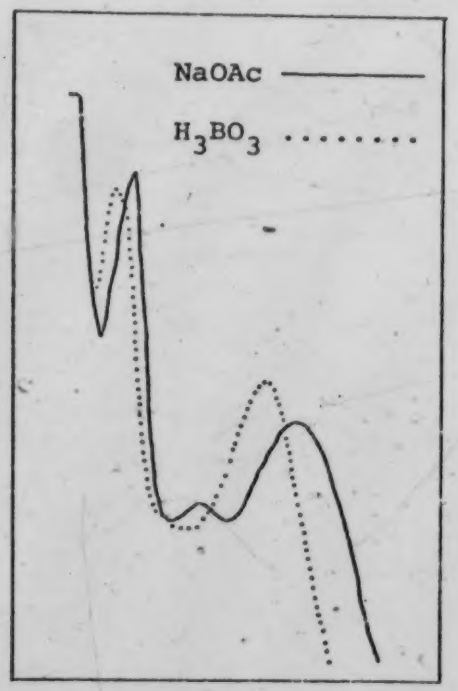
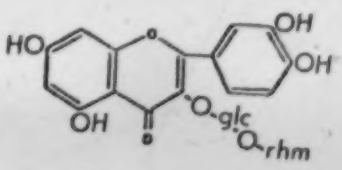
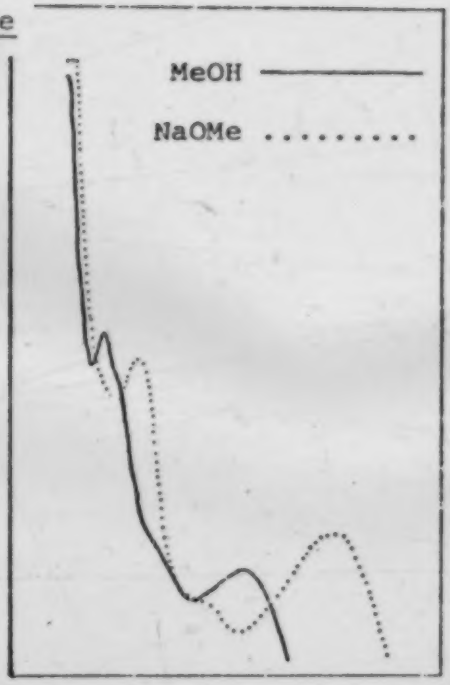


FIGURE 40.

Chromatographic and spectral data for Quercetin 3-O-glucosylrhamnoside

#31 Quercetin 3-O-glucosylrhamnoside



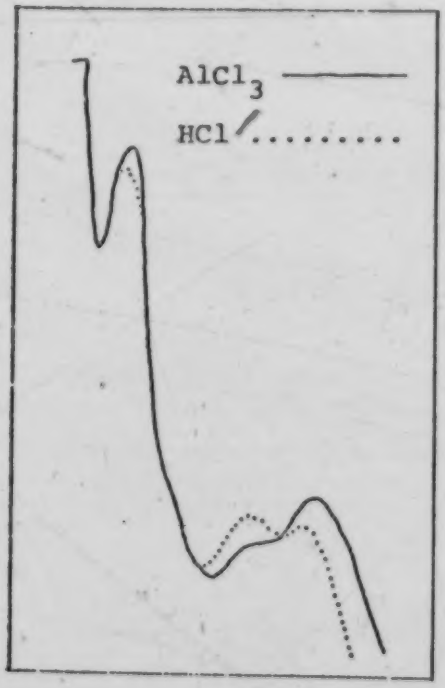


Chromatographic Data

Rf Values				Spot Colour	
BAW	H_2O	HoAc	PhOH	UV	UV/NH_3
68	20	34	79	ppl	ylw

UV Spectral Data

MeOH	256, 268sh, 356
NaOMe	280, 418
$AlCl_3$	272, 408
$AlCl_3$/HCl	268, 362
NaOAc	274, 326sh, 401
H_3BO_3	258, 368



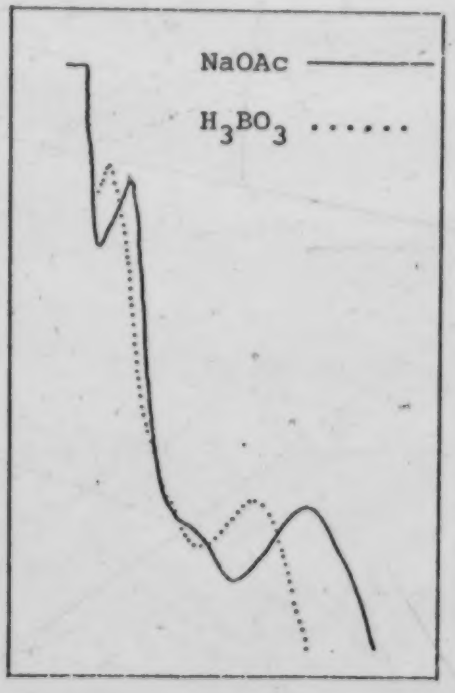
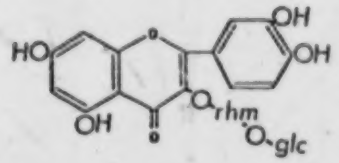


FIGURE 41.

Chromatographic and spectral data for Quercetin 3-O-rutinoside

#32 Quercetin 3-O-rutinoside

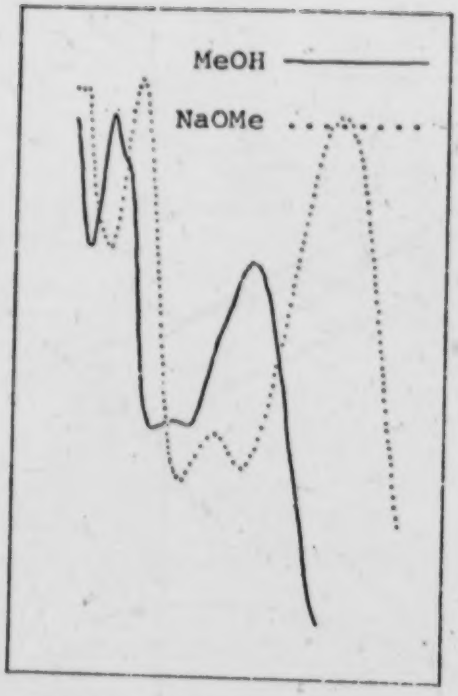


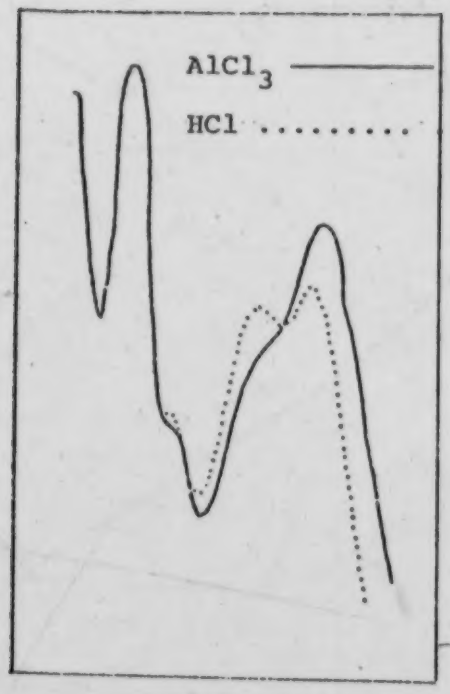
Chromatographic Data

	Rf Values			Spot Colour	
BAW	H_2O	HoAc	PhOH	UV	UV/NH_3
50	33	54	70 44	ppl	yg

UV Spectral Data

MeOh	258, 268sh, 358
NaOMe	276, 332, 419
$AlCl_3$	274, 306sh, 410
$AlCl_3$/HCl	274, 306sh, 364
NaOAc	276, 326, 408
H_3BO_3	262, 376





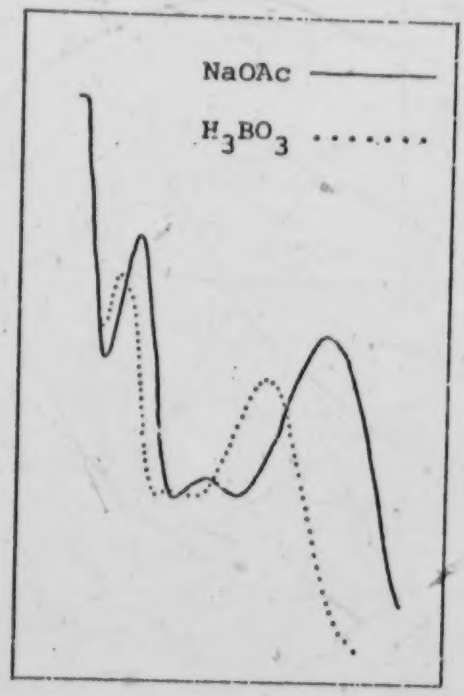
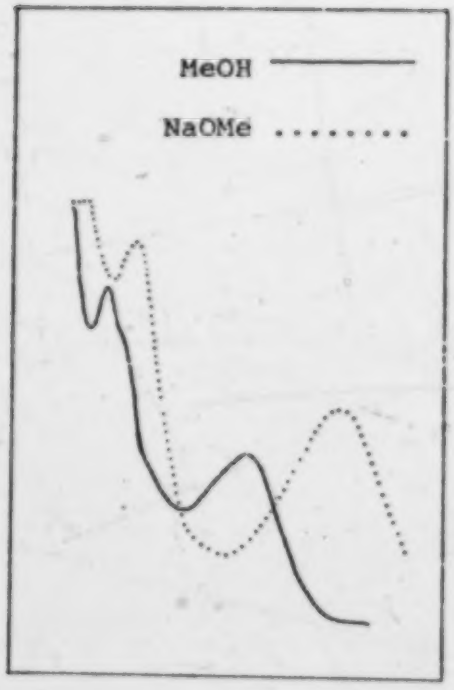


FIGURE 42.

Chromatographic and spectral data for Quercetin glycoside #33

#33 Quercetin ?

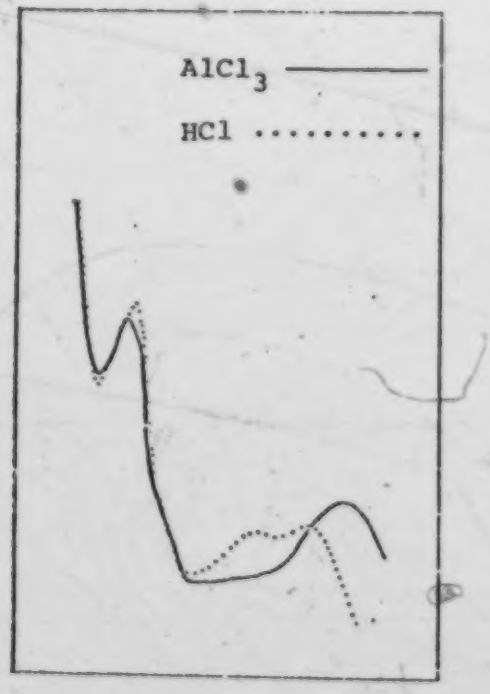


Chromatographic Data

	Rf Values			Spot Colour	
BAW	H_2O	HoAc	PhOH	UV	UV/NH_3
24	43	65	44	ppl	ylw

UV Spectral Data

MeOH	258, 268sh, 358
NaOMe	278, 422
$AlCl_3$	270, 276sh, 430
$AlCl_3$/HCl	278, 365, 404
NaOAc	262, 382
H_3BO_3	260, 372



Tables 14 and 15 show that much of the diversity of the glycosides present is due to the identity, number, and attachment of the sugar component (for example, glycosides 21-23). A total of four different sugars were found: glucose, arabinose, rhamnose, and the relatively rare xylose. No taxon had all the sugars represented; *jordalii*, for example, lacked arabinose.

The majority of the thirty-three glycosides were restricted in their occurrence. Twenty-two of the flavonoids were present in only one population (Table 16). The taxon *cusickii* had nine unique glycosides (69% of its flavonoid profile) while *jordalii* had five (50%) and *gracilis* had four unshared flavonoids (36%). The two chromosome races (48, 96) of the taxon *varians* each had two unique glycosides.

Eleven of the thirty-three total flavonoids were present in two or more populations (Figure 43). No one glycoside occurred in all the populations analyzed, although kaempferol 3-O-glucoside was found in four.

Comparisons between taxa indicated that the taxa *gracilis* and *varians* shared the largest number of compounds: luteolin 7-O-triglucoside, glycosides #15 and #17, apigenin 7-O-rutinoside, and kaempferol 3-O-glucoside. The chromosome races of the taxon *varians* shared four flavonoid glycosides: quercetin 3-O-rutinoside, glycoside #17, luteolin 7-O-glucoside, and kaempferol 3-O-

TABLE 16.

Flavonoid glycosides present in only one taxon

FLAVONOID GLYCOSIDE		TAXA				
		australis	*gracilis*	*tenuis*	*maritima* 88 race	*maritima* 99 race
?	#14	+	-	-	-	-
kaempferol 3-O-sambubioside	#19	+	-	-	-	-
quercetin 3-O-glucose-7-O-glucoside	#24	+	-	-	-	-
quercetin 3-O-sophoroside-7-O-glucoside	#25	+	-	-	-	-
quercetin 3-O-sambubioside	#26	+	-	-	-	-
quercetin 3-O-diglucosylxyloside	#27	+	-	-	-	-
quercetin 3-O-diglucosylxylosice	#28	+	-	-	-	-
quercetin 3-O-sambubioside-7-O-glucoside	#29	+	-	-	-	-
?	#33	+	-	-	-	-
apigenin 7-O-glucosylvicianoside	#7	-	+	-	-	-
?	#16	-	+	-	-	-
kaempferol 3-O-rutinoside	#20	-	+	-	-	-
quercetin 3-O-glucosylrhamnoside	#30	-	+	-	-	-
apigenin 7-O-glucoside	#1	-	-	+	-	-
apigenin 7-O-glucoside	#2	-	-	+	-	-
apigenin 7-O-diglucoside	#3	-	-	+	-	-
apigenin 7-O-sambubioside	#5	-	-	+	-	-
luteolin 7-O-diglucoside	#10	-	-	+	-	-
luteolin 7-O-glucosylrutinoside	#12	-	-	-	+	-
luteolin 7-O-rutinoside	#13	-	-	-	+	-
apigenin 7-O-vicianoside	#8	-	-	-	-	+
quercetin 3-O-glucoside	#23	-	-	-	-	+
TOTAL UNIQUE GLYCOSIDES		9	4	5	2	3
PERCENTAGE OF FLAVONOID PROFILE		45%	26%	50%	18%	30%

TABLE 43. Flavonoid glycosides present in more than one taxon

FLAVONOID GLYCOSIDE	TAXA				
	fordalii	*gracilis*	*variana*	*88 race*	*ouelebit*
quercetin 3-O-glucosylrhamnoside #31	■	■			
luteolin 7-O-triglucoside #11	■	■	■		
? #15	■	■	■		
apigenin 7-O-triglucoside #4	■	■			
quercetin 3-O-glucoside #23	■		■		■
apigenin 7-O-rutinoside #6		■	■		
? #17		■	■	■	
quercetin 3-O-rutinoside #32		■	■	■	
luteolin 7-O-glucoside #9		■	■	■	■
kaempferol 3-O-glucoside #18		■	■	■	■
quercetin 3-O-glucoside #21				■	■

glucoside.

In addition to the detailed analysis of these populations, twenty-one others, representing all seven morphological taxa, had their chromatographic profiles compared. However, no attempt was made to establish the distribution and occurrence of potential marker compounds due to the large number of flavonoids with similar chromatographic characteristics. The collections used in the flavonoid survey are listed in Table 17.

TABLE 17.

Collections used in flavonoid analysis of the *Oxytropis campestris* (L.)DC. complex

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Alaska: WJE #250, Tok Junction, June 24, 1976; WJE #271, Moose Pass, June 26, 1976; WJE #278, McKinley Park, June 28, 1976; WJE #300, mile 307, TAPS Hwy., July 3, 1976; WJE #310, mile 322, TAPS Hwy., July 4, 1976.

Alberta: WJE #021, Prospect Creek Rd., Cadomin, August 28, 1976; WJE #048, Hwy. #1, W. of Calgary, August 13, 1976; WJE #058, Kananaskis Rd., July 15, 1975; WJE #223, Prospect Creek Rd., Cadomin, June 16, 1976; WJE #108, Carthew Mt., Waterton Park, July 12, 1977.

British Columbia: WJE #344, mile 403, ALCAN Hwy., July 9, 1976.

Montana: WJE #096, Beartooth Pass, Hwy. #212, August 12, 1975; WJE #102, Goat Flats, Anaconda Wilderness, August 11, 1976; WJE #392, Mud Creek, Glacier Park, August 13, 1976; WJE #443, Glacier Co., July 9, 1977.

North Dakota: WJE #182, Glen Ullin, Morton Co., May 26, 1976.

Northwest Territories: WJE #457, Dolomite Lake, Inuvik,

TABLE 17.(cont.)

July 5, 1977; WJE #467, Rocky Hills, July 7, 1977; WJE #475, Richardson Mts., July 5, 1977.

Oregon: WJE #375, Wallowa Mts., Joseph, August 9, 1976.

Saskatchewan: WJE #195, Broadview, May 27, 1976.

South Dakota: WJE #176, Hwy. #16, Custer Co., Black Hills, May 25, 1976.

Washington: WJE #357, Hurricane Ridge, Olympic Park, August 6, 1976.

Yukon Territories: WJE #241, Kluane Lake, June 24, 1976; WJE #323, mile 82, Dempster Hwy., July 6, 1976.

CHAPTER 4.

DISCUSSION AND CONCLUSIONS

The results of the present study do not support the concept of a North American *Oxytropis campestris* (L.)DC. as suggested by various workers (Barneby, 1952; Boivin, 1967; Hultén, 1967). As presented here, a number of the taxa they relegate to the category of variety or subspecies should be given species status in light of the morphological, chemical, and cytological data (summarized in Table 18). With the exception of the taxon *davisii*, all taxa investigated have previously been recognized at the specific level (for example, *O. columbiana* St. John, 1928; *O. jordalii* Porsild, 1951). The author proposes the following treatment of the *Oxytropis campestris* complex in northwestern North America.

Oxytropis varians (Rydb.) K. Schum.

Aragallus varians Rydb., Bull. N.Y. Bot. Gard., 2:176. 1901.
Oxytropis varians (Rydb.) K. Schum., Just's Jahresb., 27:543. 1903.
Oxytropis alaskana A. Nels., Univ. Wyo. Pub. Bot., 1:120. 1926.
Oxytropis hyperborea Porsild, Sargentia, 4:53. 1943.
Oxytropis campestris (L.)DC. var. *varians* (Rydb.) Barneby, Proc. Cal. Acad. Sci. IV. 27: 253. 1952.

TABLE 18.

Synopsis of the characters of the seven taxa in the *Oxytropis campestris* (L.)DC. complex in northwestern North America

CHARACTER	TAXA							
	varians		*gracilis*	*dispar*	*cusickii*	*columbiana*	*jordalii*	*davisii*
	48 race	*96 race*						
Number of leaflets	13-45	13-23	17-33	17-25	7-17	11-17	9-25	31-51
Stipule: Dorsal Vesture	pilose, glabrate	pilose, glabrate	pilose, glabrate	densely pilose	thinly pilose, glabrate	pilose, rarely glabrate	thinly pilose, glabrate	thinly pilose, glabrate
Stipule: Marginal Vesture	ciliate, clavate processes	ciliate, clavate processes	ciliate, glabrate, clavate processes rare	ciliate, clavate processes rare	ciliate, rarely glabrate	ciliate, clavate processes rare	ciliate, clavate processes	ciliate, clavate processes
Number of flowers per raceme	10-25	8-15	6-30	8-15	6-15	6-28	6-14	10-16
Corolla colour	ochroleu-cous, whitish	ochroleu-cous, whitish	ochroleu-cous, whitish	ochroleu-cous, whitish, pink, purple	ochroleu-cous	whitish	ochroleu-cous, pink, purple	pink, purple
Corolla: Keel length (mm.)	10-12.5	11-15	10-14	12.5-14	11-14	11-14	10-11	11-12
Pod: Texture	chartaceous	char.	char.	char. to coriaceous	char. to coriaceous	char.	char.	char.
Chromosome Number (2n)	48	96	32, 48	32	48	48	32	32
Habitat	rocky hillsides, moraines, arctic & sub-arctic shores, roadsides	roadsides, gravel bars, open forests	prairies, roadsides, mountain meadows, open wood-land	prairies, wooded ravines	rockslides stony ridges, alpine & sub-alpine meadows	gravel bars stony lake or river shores	arctic-alpine ridges & meadows	gravelly stream banks & shores
Distribution	Alaska, Yukon, western N.W.T.	Alaska, eastern Siberia	Wyoming to Washington southern third of prairie provinces	North Dakota	northern & central Rocky Mts. Wallowa Mts., Ore.	northeastern Washington, northwestern Montana	central Alaska, northern Alaska & Yukon, Ogilvie & MacKenzie Mts., dis-junct to Juneau & Mtn. Park Alberta	northeastern British Columbia
Flavone aglycone: apigenin	present	present	present		absent		present	
Flavonol aglycone kaempferol	present	present	present		present		absent	

Variable in stature and pubescence; stipules pilose dorsally, the margins beset with bristly ciliae and some clavate processes; leaves 3-15 cm. long; leaflets 13-45 , subopposite or geminate; scapes ascending 3.5-24 cm. long; racemes 10-25 flowered; calyx with black and pale hairs in varying proportions, 6-8 mm. long, tube 4-6 mm., the teeth 1.5-3 mm. long; petals ochroleucous, yellowish, or white; banner 13-15 mm. long; wings 12-15 mm. long, blades 3-4 mm. wide; keel 10.5-14 mm. long, occasionally maculate; chromosome number 2n=48, 2n=96; rocky hillsides, roadsides, moraines, gravel bars, shores in Alaska, the Yukon, and the western Northwest Territories.

Holotype: Lewes River, Yukon; J.B. Tarleton 33b, 1899, (US)!

First described by Rydberg in 1901, *Oxytropis varians* is aptly named since it is variable in stature, vestiture, length of stipule blades, length of scapes and leaves, number and disposition of the leaflets, length of the flowers, and the length of the calyx. This variability has resulted in diverse taxonomic treatments of the taxon.

Within the *O. varians* complex, Porsild (1943) recognized two species in the far northwest marked by the presence or absence of paired leaflets in some of the leaves, *O. hyperborea* and *O. campestris* respectively. The author's examination of herbarium specimens and personal collections failed to sustain this separation or Porsild's taxonomic treatment of the taxa. As Barneby (1952) observed, the degree to which the leaflets are geminate varies in plants of the same collection and

PLATE 2.

Type specimen of *Oxytropis varians* (Rydb.) K. Schum.

UNITED STATES NATIONAL HERBARIUM.
DEPOSITED BY THE SMITHSONIAN INSTITUTION.
391471

PLANTS OF YUKON TERRITORY

Astragalus arcticus Hook. & Lo.
Syph.
Lewis River.
No. 334 Collection
June 25.

from the same locality and are not correlated with other characters.

Hultén (1967, 1968) also did not recognize the taxon *varians* and has referred this material from Alaska, the Yukon, and the Northwest Territories to *O. campestris* (L.)DC. subsp. *gracilis* (A. Nels.) Hult. Both Welsh (1967) and Boivin (1967) do, however, recognize the taxon as circumscribed by Barneby (1952).

The results of the present study support Barneby's concept of a morphologically distinct taxon restricted to Alaska, the Yukon, and the western MacKenzie district. Although two chromosome numbers are present in this taxon (Table 5), analysis failed to reveal significant morphological differentiation between them (Table 18). Individuals of either number are extremely variable in stature, vestiture, and flower size; it is only guard cell lengths that distinguish them. Further analysis is required in order to elucidate cryptic morphological differences.

The distribution of the two chromosome numbers of *O. varians* is plotted on Map 3. Restricted to the unglaciated regions of the far northwest, the dodecaploid (2n=96) occurs in Alaska and the extreme eastern portion of Siberia. To the south, east, and north, it is partially surrounded by hexaploid (2n=48) representatives. Considering the adaptive inferiority of strict autopolyploids in rapidly changing environments (Stebbins,

MAP 3.

Distribution of the chromosome numbers in *Oxytropis varians* (Rydb.) K.Schum. based on the author's collections, published chromosome counts, and guard cell measurements of herbarium material

2n=48 ▲

2n=96 ■

1971), the dodecaploid is possibly alloploid (*sensu* Grant, 1971) in origin. Observations of meiotic pairing would be crucial to any interpretation of the origin of the higher polyploid.

The flavonoid data listed in Tables 12 and 13 and summarized in Figure 43 indicate that the populations representing the two chromosome numbers of *O. varians* share four glycosides, 45% of the identified components of the flavonoid profile for the dodecaploid. Obviously, there is much genic and chromosomal differentiation underlying the morphological similarities. In the interest of a practical taxonomy, however, it has been decided to treat the complex as a morphological-geographical unit: *O. varians* (distribution shown on Map 4).

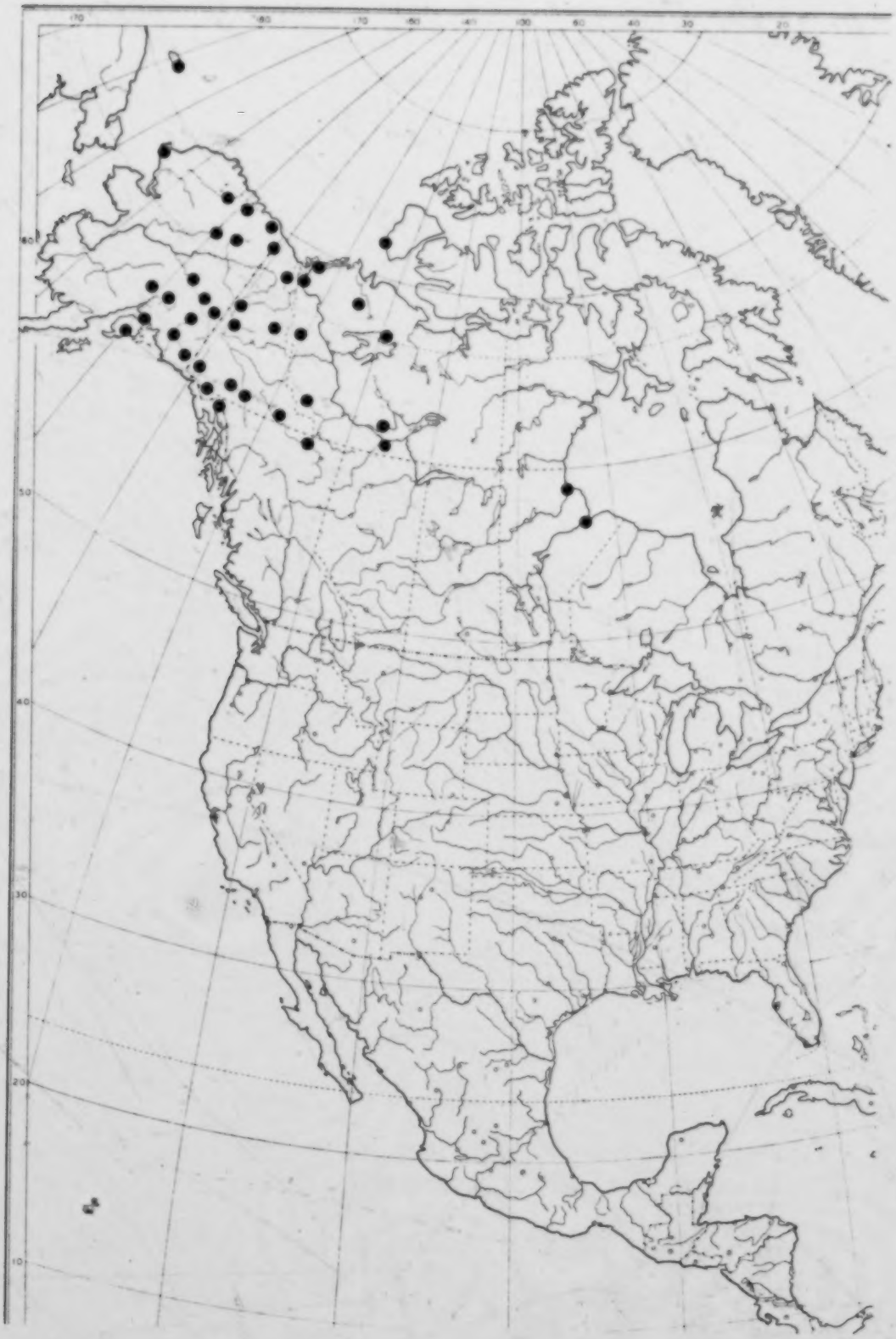
It is interesting to note that the hexaploid *O. varians* (2n=48) shares five glycosides with the tetraploid race (2n=32) of *O. gracilis*, 50% of the latter's flavonoid profile. Indeed, these two taxa share the greatest number of flavonoid glycosides among the populations analyzed. There are, though, many geographical and morphological discontinuities that warrant separation of the two taxa at the species level.

Oxytropis gracilis (A. Nels.) K. Schum. subsp. *gracilis*

Aragallus gracilis A. Nels., Erythea, 7:60. 1899.

MAP 4.

Distribution of *Oxytropis varians* (Rydb.) K.Schum. based on the author's collections and selected herbarium material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Oxytropis lambertii β Hook., Fl. Bor. Amer., 1:107. 1834.
Oxytropis monticola Gray, Proc. Amer. Acad., 20:6. 1884. *pro max parte.*
Spiesia monticola (Gray) O. Kze., Rev. Gen., 206. 1891.
Aragallus monticola (Gray) Greene, Pittonia, 3:212. 1897.
Oxytropis gracilis (A. Nels.) K. Schum., Just's Jahresb., 27:496. 1901.
Aragallus villosus Rydb., Bull. Torr. Club, 28:36. 1901.
Oxytropis villosa (Rydb.) K. Schum., Just's Jahresb., 29:543. 1903.
Aragallus luteolus Greene, Proc. Biol. Soc. Wash., 18:17. 1905.
Aragallus albertinus Greene, Proc. Biol. Soc. Wash., 18:15. 1905.
Aragallus cervinus Greene, op. cit., 16. 1905.
Aragallus macounii Greene, loc. cit., *pro parte.*
Oxytropis luteola (Greene) Piper and Beattie, Fl. N.W. Coast, 337. 1915.
Oxytropis olympica St. John, Proc. Biol. Soc. Wash., 41:103. 1928.
Oxytropis mazama St. John, op. cit., 101. 1928.
Oxytropis okanoganea St. John, op. cit., 102. 1928.
Oxytropis cascadensis St. John, op. cit., 105. 1928.
Oxytropis albertina (Greene) Rydb., Fl. Prair. & Pl., 484. 1932.
Astragalus rydbergianus Tidestr., Proc. Biol. Soc. Wash., 50:19. 1937. (*non A. villosus* Mchx.).
Astragalus albertinus (Greene) Tidestr., loc. cit. 1937.
Astragalus mazama (St. John) G.N. Jones, Univ. Wash. Pub. Bot., 7:175. 1938.
Astragalus grayanus Tidestr., in Tidestr. & Kitt., Fl. Ariz. & New Mex., 216. 1941.
Oxytropis campestris (L.)DC. var. *gracilis* (A. Nels.) Barneby, Proc. Cal. Acad. Sci. IV, 27:256. 1952.
Oxytropis campestris (L.)DC. subsp. *gracilis* (A. Nels.) Hult., Kungl. Svensk Veten. Handl., 7:1. 1967.
Oxytropis campestris (L.)DC. var. *cervinus* (Greene) Boivin, Nat. Can., 94:75. 1967.

Variable in vestiture of herbage; stipules almost glabrous to densely pilose dorsally, the free blades ciliate or eciliate; leaves somewhat dimorphic, 6-23 cm. long with 17-33 linear-oblong, lanceolate, or obovate leaflets 6-23 mm. long, commonly opposite or sub-opposite; scapes erect 10-30 cm. long; racemes 10-30 flowered; bracts pilose dorsally, shorter than to nearly twice as long as the calyx; calyx pilose or hirsute 7-9.5 mm. long, tube 4.5-6.5 mm., teeth 1.5-2.5 mm. long; corolla whitish or ochroleucous; banner 12-17 mm. long; 4-7 mm. wide; wings 10-16 mm. long, the blades oblong rarely dilated upward; keel 10-14.5 mm. long; chromosome number 2n=32, 2n=48; prairies, open woodlands, and mountain meadows from British Columbia and northwestern Washington to southwestern Manitoba and northern Colorado.

Type: Limestone Range, Black Hills, Weston Co., Wyoming; A. Nelson 2545 (GH, NY, US isotypes!), 1896.

Oxytropis gracilis subsp. *gracilis* has been known for over a century and, as Barneby (1952) notes, has had a rather chequered nomenclatural history. The *O. campestris* of early authors undoubtedly was this taxon. *O. gracilis* was first segregated from the European *O. campestris* and from *O. lambertii* in Gray's second revision (1884), where it received the name *O. monticola*. This species was, unfortunately, based on six collections which were not conspecific; consequently, it has been misunderstood by many taxonomists. The type of *O. monticola*, selected by C.L. Porter because it was the first collection cited by Gray in his revision, is actually *O. viscida*. The first validly published name and description of this taxon was *Aragallus gracilis* by Aven Nelson (1899).

PLATE 3.

Type specimen of *Oxytropis gracilis* (A. Nels.) K. Schum. subsp. *gracilis*

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no. 2575 FLORA OF WYOMING.

Orazellus gracilis Rydb. Nelson mss.
Limestone Range, Newcastle
coll. Aven Nelson. July 20, 1896.

Herb. University of Wyoming.

O. gracilis subsp. *gracilis*, typical of the majority of species in this genus, is highly variable with respect to vestiture, leaf size, and, to some extent, flower size. As in *O. varians*, this variability has resulted in the naming of numerous taxa often based on unstable and uncorrelated characters. Rydberg (1901), for example, described villous specimens of *O. gracilis* subsp. *gracilis* as *Aragallus villosus*. Later workers demonstrated that the silky and glabrescent states often exhibit many intermediate forms occurring in the same locality and even in the same collection.

East of the continental divide, subsp. *gracilis* forms a particularly coherent unit characterized by small flowers with whitish or ochroleucous petals and numerous leaflets. Map 5 shows its distribution. The cytological data, presented in Table 5, indicate that these plants also possess the same chromosome number, 2n=32. Eleven flavone and flavonol glycosides were identified in the sample representing this taxon (Table 10). Table 16 shows that 36% of the glycosides are unique to subsp. *gracilis*. This represents a substantial degree of chemical uniqueness and reinforces the concept of a morphologically, cytologically, and geographically distinctive taxon east of the continental divide.

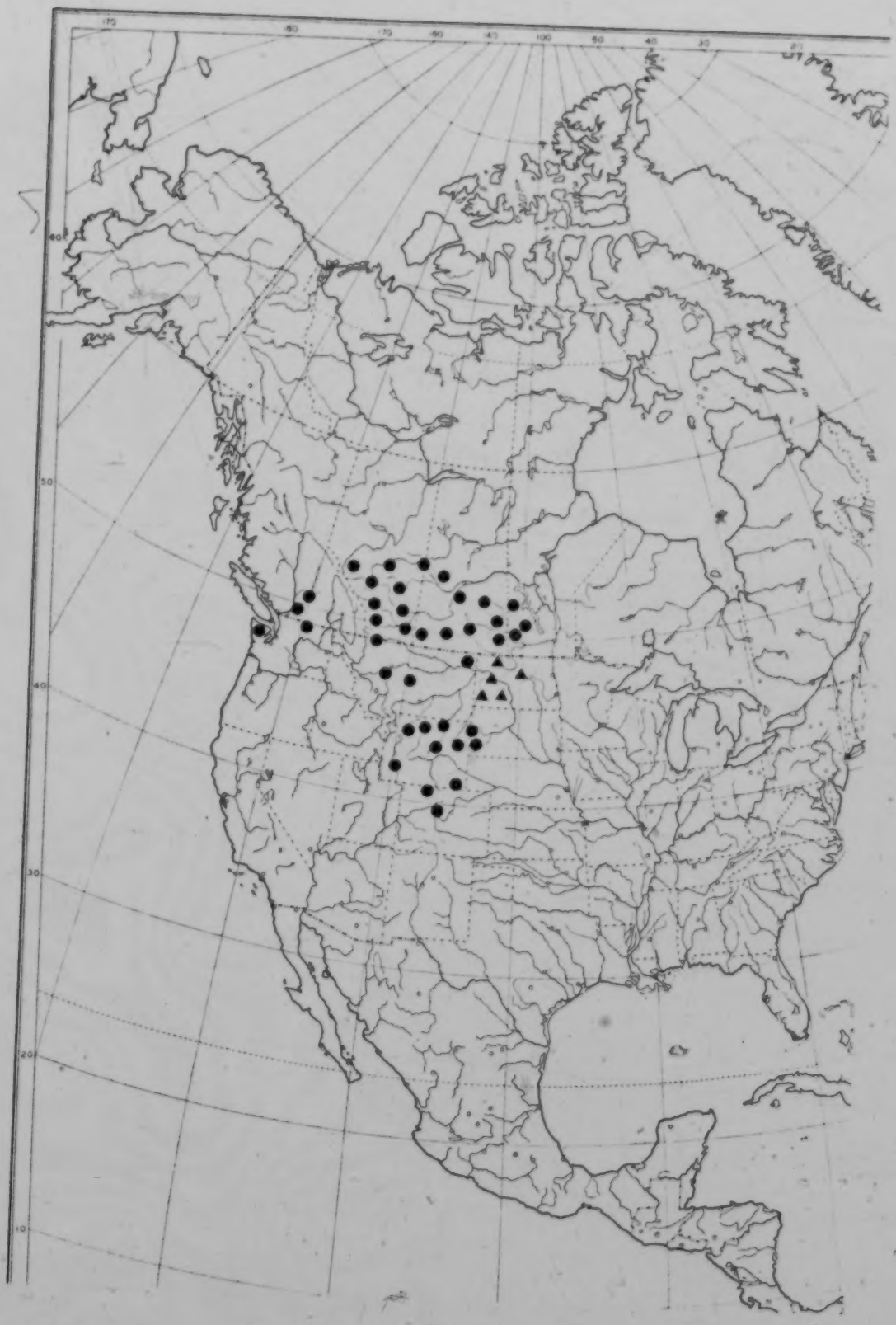
West of the continental divide, the situation in subsp. *gracilis* becomes quite complicated. St. John

MAP 5.

Distribution of *Oxytropis gracilis* (A.Nels.) K.Schum. based on the author's collections and selected herbarium material

● subsp. *gracilis*

▲ subsp. *dispar* (A.Nels.) Elisens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(1928) in his revision of the loco weeds in Washington, distinguished four species (*Oxytropis luteola*, *O. mazama*, *O. olympica*, and *O. cascadensis*) from northern Washington on the basis of calyx size and stipule pubescence. Representatives of these taxa while not exactly alike, do intergrade morphologically and also with subsp. *gracilis* east of the divide. A similar situation is found in the plants along the Okanagan River in northern Washington and British Columbia described by St. John (1928) as *O. okanaganea*. In its extreme state with tall erect villous scapes, densely pilose stipules, few leaflets, and large flowered racemes, *O. okanaganea* St. John is distinct from subsp. *gracilis*. However, many of the herbarium specimens examined intergrade with subsp. *gracilis* and, at the present time, the author agrees with Barneby (1952) who lists it as a synonym of var. *gracilis*.

Ledingham (1960) reported a chromosome count of 2n=48 for material representing *O. okanaganea* St. John (Table 3). The cytological data of the present study (Table 5) give a similar count for *O. olympica* St. John. Indeed, the guard cell measurements from herbarium specimens (Table 8) indicate that all representatives of *O. gracilis* subsp. *gracilis* from west of the continental divide are 2n=48. This is in distinct contrast to the 2n=32 found uniformly in populations east of the divide. Although no detailed flavonoid studies were carried out

on this material, the cytological and morphological data presented here suggest that subsp. *gracilis* is comprised of at least two distinct entities. However, as with *O. varians*, the author has decided not to subdivide *O. gracilis* subsp. *gracilis*.

Oxytropis gracilis (A. Nels.) K. Schum. subsp. *dispar* (A. Nels.) Elisens *comb.* and *stat. nov.*

based on
Aragallus dispar A. Nels., Erythea, 7:61. 1899.

Oxytropis campestris (L.)DC. var. *dispar* (A. Nels.) Barneby, Proc. Cal. Acad. Sci. IV, 27:263. 1952.

Herbage densely silk-pilose, the stipules usually concealed by vestiture; leaves often dimorphic with 17-25 linear lanceolate or ovate leaflets to 2 cm. long; scapes erect, 7-19 cm. long; racemes 8-15 flowered; calyx 8-9 mm. long, the tube 6-6.5 mm., teeth 2-2.5 mm. long; petals purple, blue, pink, white, or ochroleucous; the banner 17-19 mm. long, 6-8 mm. wide; wings 14-16 mm. long, the blades dilated upward and 4.5-6 mm. wide near the apex; keel 12-13 mm. long; pod coriaceous; chromosome number 2n=32; prairies or brushy places along ravines in North Dakota.

Holotype: Dickinson, Stark Co., North Dakota; 1896; Mrs. Cook (RM)!

O. gracilis subsp. *dispar* was first described by Aven Nelson (1899) as *Aragallus dispar*. The epithet *dispar* refers to the occasional dimorphism of the leaves. Subsequent workers have noted that this "key" character has been overstressed since it appears occasionally in subsp. *gracilis* and in *O. varians*. The diagnostic char-

PLATE 4.

Type specimen of *Oxytropis gracilis* (A. Nels.) K. Schum. subsp. *dispar* (A. Nels.) Elisens

Mrs. L. R. Cook, 1877.

acters of the taxon, the polychrome colouration of the flowers and the somewhat coriaceous texture of the pod, have indicated to Porter (1951) and Welsh (1960) that subsp. *diapar* originated as a fertile hybrid between *O. gracilis* subsp. *gracilis* and *O. lambertii*. Although no detailed flavonoid data were obtained, the cytological data of the present study (Table 5) does not support their hybridization hypothesis. *O. gracilis* subsp. *dispar* has a chromosome number of 2n=32 while Ledingham (1957) reports 2n=48 for *O. lambertii*.

Subspecies *dispar* is cytologically, ecologically, and morphologically similar to subsp. *gracilis* yet it is geographically distinct and morphologically recognizable. Following Davis and Heywood (1963), it is best categorized at the subspecific level.

Oxytropis cusickii Greenm.

Oxytropis cusickii Greenm., Erythea, 7:116. 1899.
Aragallus alpicola Rydb., Mem. N.Y. Bot. Gard., 1:252. 1900.
Oxytropis alpicola (Rydb.) Jones, Mont. Bot. Notes, 37. 1910. *non* Turcz. (1842).
Oxytropis rydbergii A. Nels., Univ. Wyo. Pub. Bot., 1:117. 1926.
Oxytropis paysoniana A. Nels., Univ. Wyo. Pub. Bot., 1:119. 1926.
Astragalus rydbergianus Tidestr., Proc. Biol. Soc. Wash., 50:19. 1937. (*non A. villosus* Mchx.).
Astragalus alpicola (Rydb.) Tidestr., Proc. Biol. Soc. Wash., 50:19. 1937.
Oxytropis campestris (L.)DC. var. *rydbergii* (A. Nels.) R.J. Davis, Madrono, 11:144. 1951.

Oxytropis campestris (L.)DC. var. *cusickii* (Greenm.) Barneby, Proc. Cal. Acad. Sci. IV, 27:261. 1952.

Low plants; densely or thinly pilose throughout; stipules glabrous or sparingly pilose toward the base, the free blades ciliate or eciliate; leaves 1.5-12 cm. long with 7-15 leaflets 3-5 mm. long; scapes erect, arcuate-ascending or prostrate, 2.5-15 cm. long; racemes 3-15 flowered; bracts pilose dorsally or somewhat glabrescent; calyx 7-9 mm. long with dark and pale haris; the teeth 2-3 mm. long; petals ochroleucous, concolourous, or keel sometimes maculate; banner 14-18 mm. long; keel 11-12.5 mm. long; chromosome number 2n=48; rock slides, stony ridges, and alpine and sub-alpine meadows between 7,000-11,000 ft. in the Rocky Mountains from northern Colorado to Alberta-British Columbia, Wallowa Mts., Oregon, Wenatchee Mts., Washington.

Types: alpine summits of the Wallowa Mountains, eastern Oregon; 1898, Cusick 1365 (GH), 2095 (GH, ND, UC, US)!

Oxytropis cusickii Greenm. was first described in 1899, one year prior to *Aragallus alpicola* Rydb. This latter synonym appears to represent a more condensed and compressed alpine state generally found in the northern part of *O. cusickii's* range (Map 6), and is not sufficiently distinct to warrant taxonomic recognition.

Barneby (1952) remarks that *O. cusickii* is intimately related to *O. gracilis* subsp. *gracilis* differing principally in the relatively few leaflets per leaf and its alpine habitat. In the southern part of its range, *O. cusickii* does show several morphological similarities

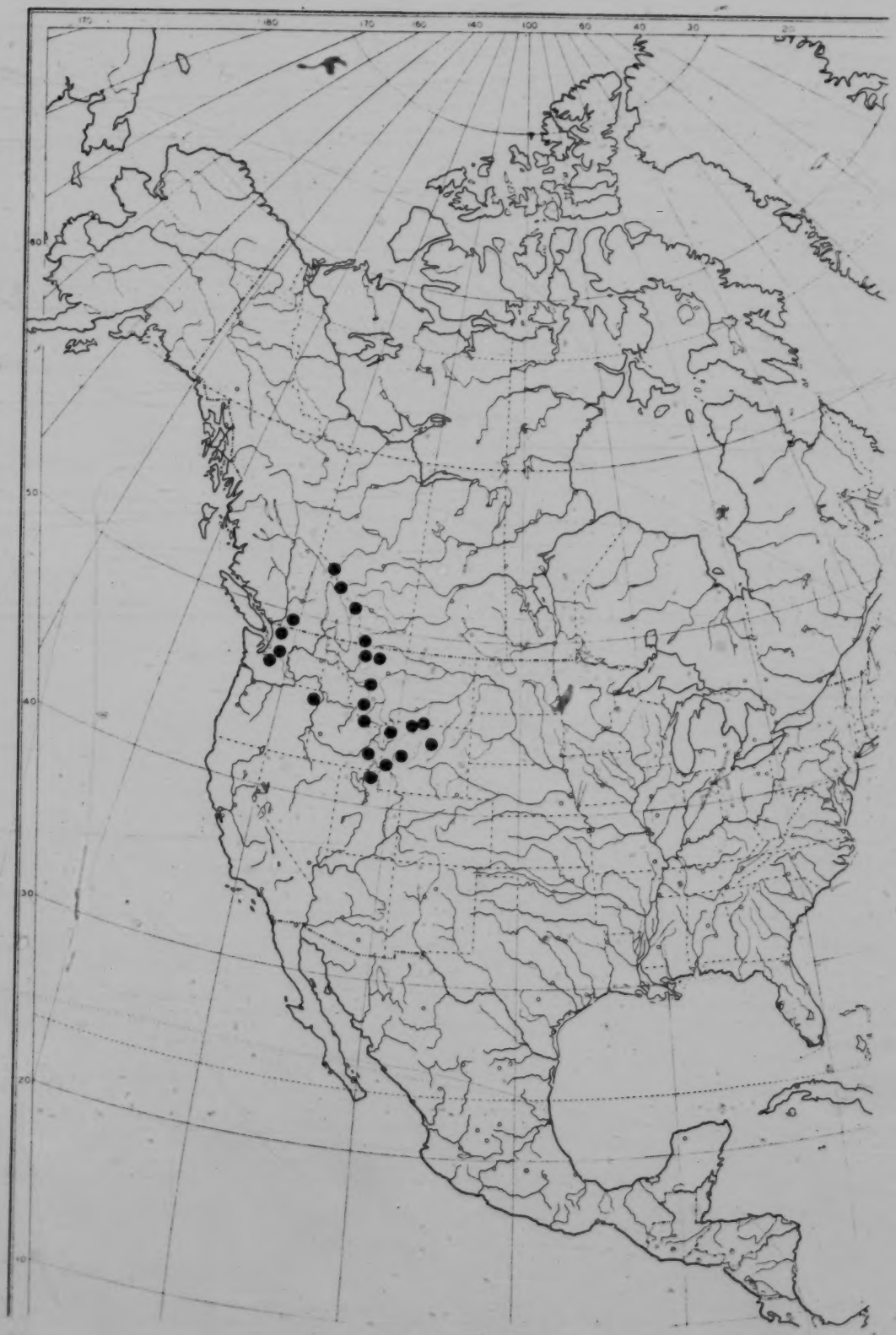
PLATE 5.

Type specimen of *Oxytropis cusickii* Greenm.

ISOTYPE

MAP 6.

Distribution of *Oxytropis cusickii* Greenm. based on the author's collections and selected herbarium material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but it consistently has a different chromosome number (2n= 48) and a radically different flavonoid profile (Table 9) than *O. gracilis* subsp. *gracilis*. The preponderance of flavonol glycosides (often with xylose as a sugar component) is unlike any other flavonoid profile analyzed in the present study. The data in Table 16 indicate that almost 70% of *O. cusickii's* glycosides were unique, occurring in no other taxa. *O. gracilis* subsp. *gracilis* and *O. cusickii* shared only one flavonol glycoside, kaempferol 3-O-glucoside. These data considered, it seems entirely appropriate to reelevate *O. cusickii* to specific status.

Morphologically and ecologically, it is often difficult to distinguish *O. sericea* Nutt. var. *spicata* (Hook.) Barneby from *O. cusickii* where they are sympatric. Generally, *O. sericea* has a thickly coriaceous pod but variability in thickness is common and has resulted in taxonomic confusion. Furthermore, Ledingham (1957, 1960) and Ledingham and Fahselt (1964) have reported chromosome numbers for *O. sericea* var. *spicata* as 2n=48. In view of the findings of the present study, the relationship between these two taxa should be reinvestigated.

Oxytropis columbiana St. John

Oxytropis columbiana St. John, Proc. Biol. Soc. Wash., 41:100. 1928.

Oxytropis campestris (L.)DC. var. *columbiana* (St. John) Barneby, Leafl. West. Bot., 5:111. 1951.

Robust, on a heavy taproot; stipules prevailingly pilose dorsally, the free blades 6-13 mm. long; leaves 8-17 cm. long with 11-17 broadly lanceolate-oblong to narrowly elliptic leaflets 9-30 mm. long; scapes erect 20-30 cm. long; racemes 10-28 flowered; calyx silky-pilose with many dark hairs, 7.5-10 mm. long, the tube 5-6.5 mm., teeth 2.5-4 mm. long; corolla white, the banner veined and the keel maculate with purplish-blue, banner oblanceolate-ovate 15.5-20 mm. long, 6 mm. wide; wings 13-18 mm. long, blades 9-11.5 mm. long, 3-4 mm. wide; keel 12-17 mm. long; chromosome number 2n=48; riparian habitats along the Columbia River in northeastern Washington, and around Flathead Lake in northwestern Montana.

Type: gravelly beach of Columbia River, near Marcus, Stevens Co., Washington, 1926, St. John 6482 (WTC, GH)!

Somewhat intermediate between *O. gracilis* subsp. *gracilis* and *O. sericea*, *O. columbiana* was first described by St. John (1928). It shares the white flowers, conspicuously maculate keel, greater stature, and chromosome number (2n=48) with *O. sericea* while its pod texture and flower size resemble *O. gracilis* subsp. *gracilis*. Its distribution (Map 7), habitat, and ease of recognition, however, reinforce St. John's decision to accord it specific status.

In some respects *O. columbiana* is similar to *O. okanaganea* St. John, discussed as a synonym of *O. gracilis* subsp. *gracilis*. They share the fewer leaflets

PLATE 6.

Type specimen of *Oxytropis columbiana* St. John

Negative No. 8959
Herbaria of the
Arnold Arboretum and Gray Herbarium
Harvard University, Cambridge, Mass.
U.S.A.

GRAY HERBARIUM HARVARD UNIVERSITY

ISOTYPE

WASHINGTON

Oxytropis columbiana St.John, n. sp.
gravelly beach of Columbia River,
Marcus, Stevens Co.,
standard and wings white with delicate
blue veins, keel bluish-purple blotched
Harold St.John 6482. June 27, 1924.

MAP 7.

Distribution of *Oxytropis columbiana* St. John based on the author's collections and selected herbarium material

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per leaf, broad wing petals, robust habit, geographical range, and chromosome number (Ledingham, 1957). This is further evidence indicative of the need for revision of *O. gracilis* subsp. *gracilis* found west of the continental divide.

Oxytropis jordalii Porsild subsp. *jordalii*

Oxytropis jordalii Porsild, Canad. Field-Nat., 65:77. 1951.
Oxytropis campestris (L.)DC. var. *jordalii* (Porsild) Welsh, Leaf. West. Bot., 10: 25. 1963.
Oxytropis campestris (L.)DC. subsp. *jordalii* (Porsild) Hult., Kungl. Svensk Veten. Handl., 7:1. 1967.

Plants caespitose from a branching caudex; leaves 6-10 cm. long; leaflets narrowly lanceolate, subinvolute, variable in vestiture; scape purplish-green, appressed strigose, 10-14 cm. long; stipules pilose dorsally with clavate processes; inflorescence capitate to sub-capitate, 6-12 flowered; calyx campanulate, 4-5 mm. long, the teeth 1.5-2 mm. long, with black and pale hairs; corolla pink, purple, yellowish, less than 14 mm. long; keel 10-11.5 mm. long, often maculate; chromosome number, 2n=32; dry rock ridges, open spruce woodlands in north-central Alaska and Yukon, MacKenzie Mts., N.W.T., Juneau, Alaska, disjunct to Mountain Park, Alberta.

Holotype: open spruce woods near Arctic Village, Brooks Range, Alaska; 1950, L.H. Jordal 3580 (CAN)!

Oxytropis jordalii subsp. *jordalii*, described by

PLATE 7.

Type specimen of *Oxytropis jordalii* Porsild subsp. *jordalii*

D. Jordalii Hitz
sched. type

REVISION BY A. E. Porsild 19 52

PLANTS OF THE BROOKS RANGE, ALASKA

Oxytropis

Scattered in dry, open subalpine spruce forest. Flowers creamy white. S shore of Old John Lake

[illegible] leg. [illegible] Jul. 10-20

202678

TYPE
Indexed

Porsild (1951), was named after L.H. Jordal who collected extensively in the Brooks Range. Distinctive with its few flowered inflorescence, small flowers and few leaflets, it has been held at least varietally distinct by subsequent workers (Welsh, 1963; Boivin, 1967; Hultén, 1967).

Porsild (1951) and Welsh (1967) suggest that it may be related to *O. terrae-novae* Fern. of the eastern arctic which it resembles in pod size and texture, and occasional flower colour (purple). However, apart from the distributional difference, it differs substantially from this taxon in the size of its flowers, and its chromosome number, 2n=32. *O. terrae-novae* has a chromosome number of 2n=48 (Hedberg, 1967).

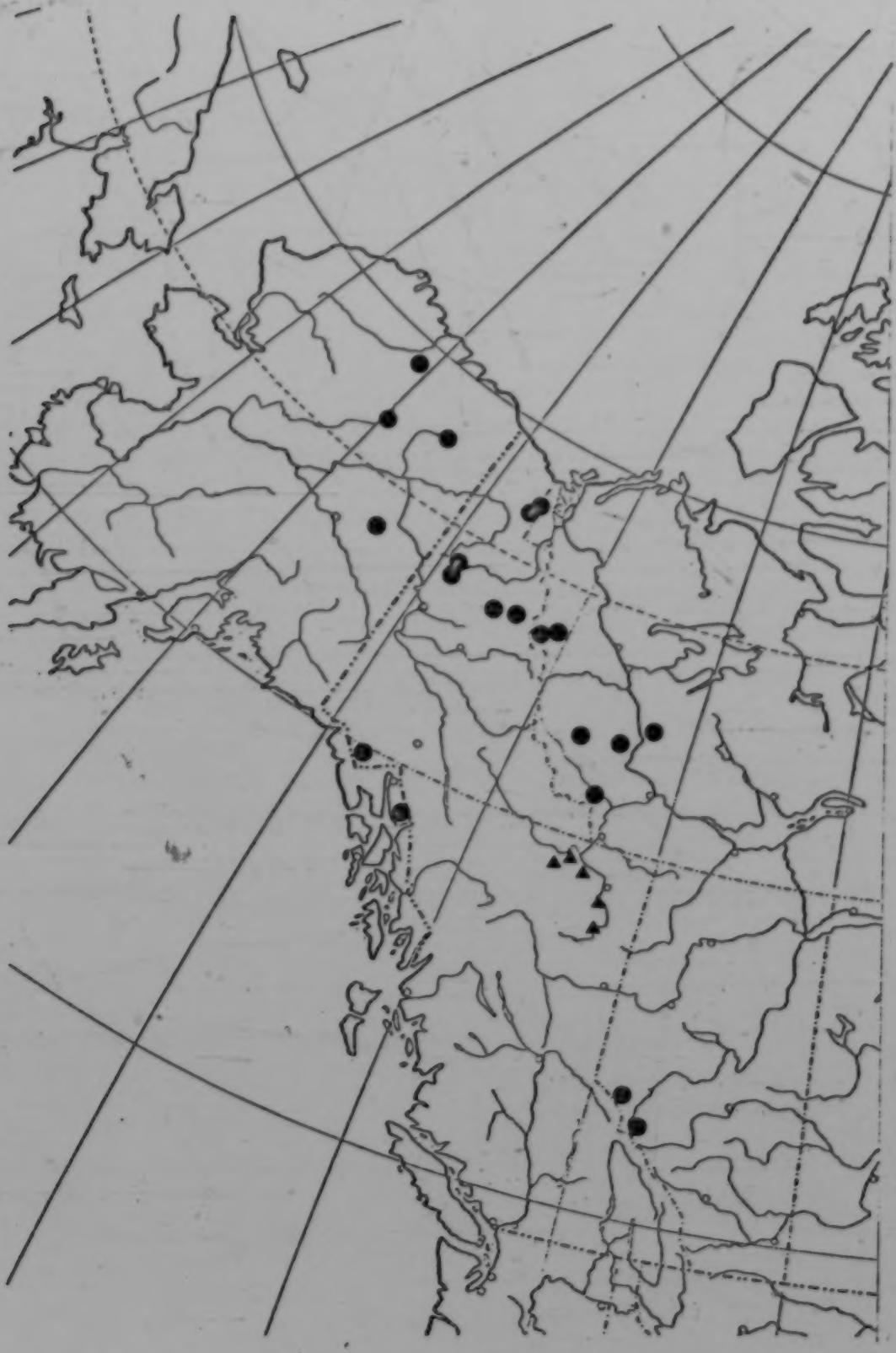
Alternatively, Hultén (1968) believes that subsp. *jordalii* is closely related to *O. campestris* (L.)DC. subsp. *sordida* (Willd.) Wahlenb. (2n=48) from northern Eurasia. Besides being different in chromosome number (Jalas, 1950; Laane, 1966), the taxon *sordida* is larger flowered and possesses more leaflets (Tutin and Heywood, 1968). *O. jordalii* subsp. *jordalii* is, thus, geographically, morphologically, and cytologically distinctive. In addition, it occurs in localities (Map 8) that were unglaciated during the Pleistocene (Geological Survey of Canada, 1968): Ogilvie Mts., Yukon; White Mts., Alaska; MacKenzie Mts., N.W.T.; and Mountain Park, Alberta

MAP 8.

Distribution of *Oxytropis jordalii* Porsild based on the author's collections and selected herbarium material

● subsp. *jordalii*

▲ subsp. *davisii* (Welsh) Elisens



(Packer and Vitt, 1974). It has also been collected near Juneau where glacial survival is suggested by Heusser's (1954) report of *Oxytropis* species on a nunatak in the Juneau ice field.

Flavonoid data from samples collected in the Mountain Park, Alberta locality (Table 11) indicate that subsp. *jordalii* has a unique flavonoid profile, comprised almost exclusively of flavone glycosides. It lacked kaempferol glycosides which were found in the other taxa analyzed. Thus, the chemical data is in agreement with the other findings of the present study which support *O. jordalii* subsp. *jordalii* as a distinctive taxon and probable glacial relict.

O. jordalii subsp. *jordalii* has both yellow flowered and pink-purple flowered forms which often intergrade depending on the locality. In the west-east transect from the Brooks Range through the British Mts. to the Richardson Mts., Welsh (pers. comm.) observed a clinal change in petal colour from yellow to pink-purple, respectively. This observation, reinforced by the author's field and herbarium studies, makes taxonomic recognition based on petal colour impractical.

Oxytropis jordalii Porsild subsp. *davisii* (Welsh) Elisens *comb.* and *stat. nov.*

based on
Oxytropis campestris (L.)DC. var. *davisii* Welsh, Leafl. West. Bot., 10:25. 1963.

Acaulescent herbs from a branching caudex; leaves pinnate, 4-10 cm. long; leaflets 25-51, ovate to lanceolate, some fasiculate 5-9 mm. long, 2-3 mm. broad, acute, pilose above and below with simple hairs; leaf-rachis and petiole grooved ventrally, strigulose to pilose; stipules 12-14 mm. long, the free ends 5-6 mm. long, sparsely pilose, ciliate, clavate processes often present; scape 5-14 cm. long, strigulose; raceme 2-4 cm. long, 10-16 flowered; petals pink-purple; calyx cylindric, with dark and light hairs, tube 4.2-4.7 mm. long, teeth 1.5-2 mm. long; chromosome number, 2n=32; gravelly disturbed habitats in northeastern British Columbia.

Holotype: mile 403.4, ALCAN Hwy., British Columbia; 1962, R.J. Davis 6076 (BRY)!

O. jordalii subsp. *davisii* was first described as a variety of *O. campestris* by Welsh (1963). Distinguished by commonly verticellate leaflets and pink-purple flowers, it demonstrates affinity with subsp. *jordalii* by its chromosome number (2n=32), pink-purple flowers, and small papery legumes. Subspecies *davisii* is restricted to the area around northeastern British Columbia (Map 8) where its occurrence suggests Pleistocene survival. No detailed flavonoid data was obtained.

PLATE 8.

Type specimen of *Oxytropis jordalii* Porsild subsp. *davisii* (Welsh) Elisens

Astragalus canadensis L. var. mollis Torr. & Gray, var. nov.

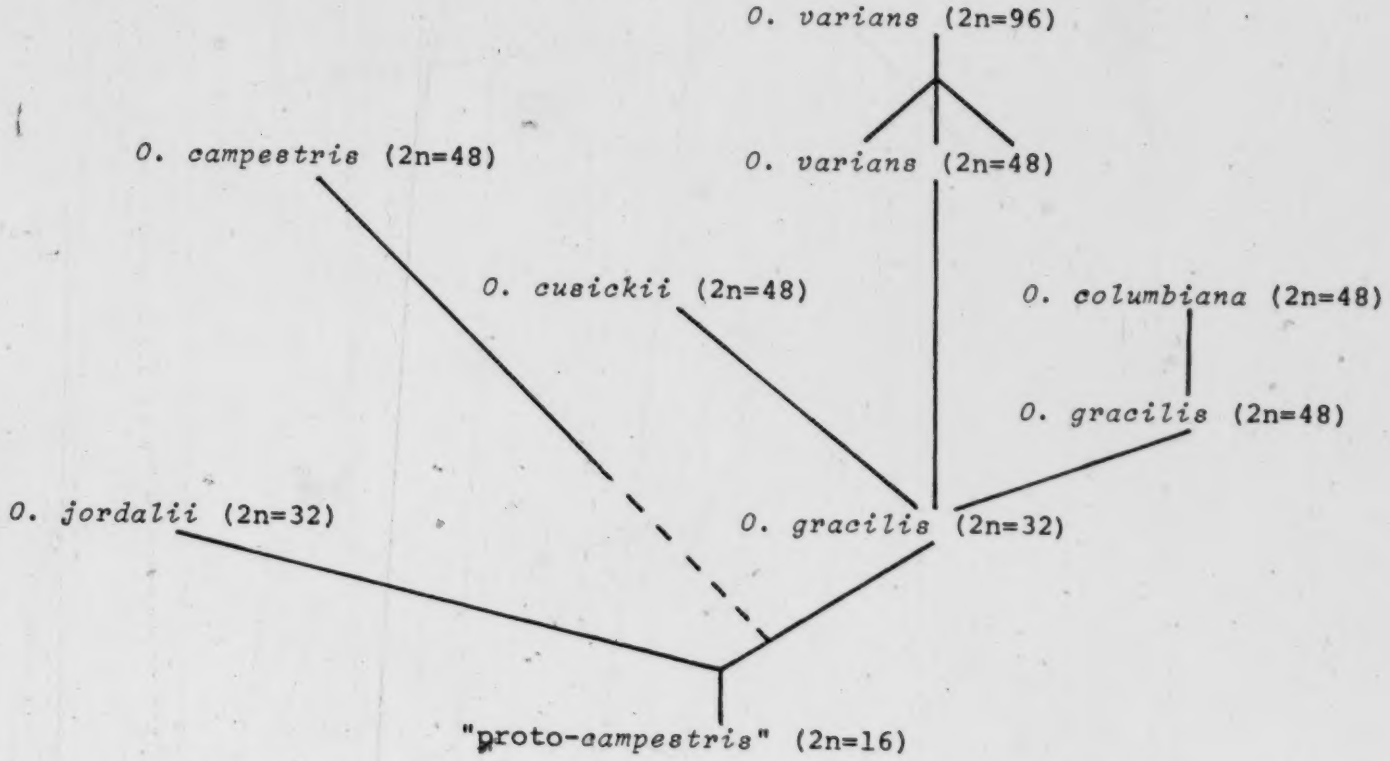
Across the Fraser east from the [illegible] on the Yanks Peninsula, in a meadow [illegible] where the soil is [illegible] 11.1 miles west of [illegible] 120° W.

May 2, 1925. [illegible]

The cytological data of the present study and the distribution of the taxa (Maps 4-8) suggest that *Oxytropis campestris sensu* Barneby (1952) and Welsh (1963) represents a mature polyploid complex (Stebbins, 1971) which has undergone several cycles of polyploidization followed by periods of diversification and differentiation. Since trends of polyploidy are generally from lower to higher levels, polyploid complexes are particularly useful in analysis of problems of plant geography and phylogeny. Stebbins (1971) states that most mature complexes originated during the Pliocene or Pleistocene. Indeed, the relative antiquity of this complex is indicated by the fact that there is no extant diploid (2n=16) *Oxytropis* similar to any of the taxa. The species with the lowest ploidy level (2n=32) in the complex, *O. jordalii* and *O. gracilis*, represent the morphological, geographical, and ecological extremes. The variable *O. gracilis* with its many leaflets, numerous ochroleucous, whitish, or pinkish flowers, and small chartaceous pods is probably most similar to a hypothetical "proto-*campestris*" (Figure 44). Survival south of the glacial margin is suggested by its present distribution. On the other hand, the low-statured, alpine taxon *O. jordalii*, with 6-12 small flowers per raceme, is ecologically and morphologically specialized. Its narrowly restricted, widely disjunct distribution, confined principally to unglaciated areas, suggests that

FIGURE 44.

Hypothetical view of the relationships in the *Oxytropis campestris* (L.) DC. complex in northwestern North America



it could be considered a patroendemic (Favarger and Contandriopoulos, 1961).

Morphological similarity (for example, the large number of leaflets, numerous flowers, small chartaceous pods) indicates that *O. varians* (2n=48, 96) and the Eurasiatic *O. campestris* (2n=48) are closely related to *O. gracilis* (2n=32, 48). The data of the present study, however, suggest that these three taxa diverged ecologically, geographically, and cytologically and have had very different evolutionary histories. The changing environments and subsequent contraction and intermixing of floras characteristic of the Quarternary might explain the relatively rapid evolutionary diversification within this polyploid complex. For example, the dodecaploid race of *O. varians* is possibly of recent hybrid origin and is still expanding its range.

In marked contrast, the differentiation of *O. cusickii* (2n=48) and *O. columbiana* (2n=48) from *O. gracilis* was, perhaps, pre-Pleistocene and a result of the late Tertiary orogenies in western North America. This long period of isolation and evolution might explain the morphological and ecological distinctiveness of these taxa.

The present investigation does not presume to have resolved all the problems in this widespread and polymorphic complex. It does, however, provide some guidance for an appropriate reclassification. Neither the

modern general practice of recognizing only a single highly variable species nor that of older workers, who recognized many species, was adopted. As is so often the outcome of systematic research, a middle course has been preferred.

Key to the *Oxytropis campestris* complex in northwestern North America

a_1 Stipules generally bearing clavate processes on the margins of the free blades; plants found north of 56° N. (except locally in the Alberta Rockies); Alaska, northern British Columbia to western MacKenzie district, N.W.T.
.....b

b_1 leaflets commonly whorled; corolla pink, purple; plants of gravelly disturbed habitats in northeastern British Columbia
.....*Oxytropis jordalii* subsp. *davisii*

b_2 leaflets not whorled; corolla yellow, white, or, if pink-purple, the distribution not as above
.....c

c_1 racemes 10-25 flowered; flowers mostly 12-17 mm. long; leaflets 19-45
.....*Oxytropis varians*

c_2 racemes 6-12 flowered; flowers mostly 14 mm. long or less; leaflets 9-21
...*Oxytropis jordalii* subsp. *jordalii*

a_2 Stipules generally lacking clavate processes on the margins of the free blades; plants found south of 56° N.; British Columbia, Oregon to Manitoba, northern Colorado
.....d

d_1 leaflets 7-17; plants of low alpine habitats in the Rocky Mountains or riparian habitats in northeastern Washington and northwestern Montana

.....e

e_1 petals white, blue-veined, with prominently maculate keel; scapes 13-30 cm.; tall plants of riparian habitats in northeastern Washington and northwestern Montana

.....*Oxytropis columbiana*

e_2 petals yellowish, rarely, if ever, maculate; scapes 5-19 cm.; low alpine plants of the Rocky Mountains

.....*Oxytropis cusickii*

d_2 leaflets 17-33, or, if less, than plants of middle elevations in northwestern Washington and British Columbia; plants of prairies, open woodland, or mountain meadows

.....f

f_1 corolla pink, purple, or polychrome; pod coriaceous; prairies of North Dakota

.....*Oxytropis gracilis* subsp. *dispar*

f_2 corolla whitish or ochroleucous; pod chartaceous; prairies, open woodland, and mountain meadows from British Columbia to Manitoba, south to Colorado

...*Oxytropis gracilis* subsp. *gracilis*

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APPENDIX

REPRESENTATIVE SPECIMENS

Oxytropis varians (Rydb.) K. Schum.

Alaska: Jago River, *J.E. Cantlon & W.T. Gillis #57-743*, (CAN); Chitina River, *H.M. Laing #125*, (CAN); Lake Schrader, north slope, *L.A. Spetzman #518*, (CAN); Umiat, *I.L. Wiggins #13878*, (CAN); Fairbanks, *E. Scamman #1654*, (GH); Firth and Mancha Rivers, *E. Hulten #62767*, (BRY); Ogotoruk Creek, *J.G. Packer #2582*, (ALTA); Richardson Hwy., *E. Scamman #4622*, (GH); Gulkana, *E. Scamman #4547*, (GH).

British Columbia: Cassiar, *J.W. Eastham #389*, (CAN).

Manitoba: Churchill, *G. M. Keleher #31*, (CAN).

Northwest Territories: Hayes River, *H.J. Scoggan #5893*, (CAN); Ewariege Lake, *V. Hawley s.n.*, (CAN); Richardson Mts., *J.G. Packer #1371*, (ALTA); Dolomite Lake, Inuvik, *W.J. Elisens #460*, (ALTA); Great Bear Lake, *A.E. and R.T. Porsild #5328*, (CAN).

Yukon Territories: South shore Kluane Lake, *W.J. Elisens #234*, (ALTA); Bear Creek, mile 1021 ALCAN Hwy., *H.M. Raup, W.H. Drury and K.A. Raup #13136*, (CAN); Miles canyon, Whitehorse, *M.O. Malte #336*, (CAN); Haines Rd., Dezadeash, *A.E. and R.T. Porsild #22308*, (CAN).

Oxytropis gracilis (A. Nels.) K. Schum. subsp. *gracilis*

Alberta: Pincher Creek, *E.H. Moss #114*, (GH); Blairmore, *A.S. Pease #22545*, (GH); west of Calgary, *W.C. McCalla #8749*, (GH); Entrance, *M.G. Dumais & K. Anderson #2450*, (CAN).

British Columbia: Keremeos, *H.J. Scoggan #16030*, (CAN); Savona, *C.L. Hitchcock & J.S. Martin #7396*, (GH); Kamloops, *J.W. & E.M. Thompson #45*, (CAN).

Colorado: Fraser, Grand Co., *S.L. Welsh & L.A. Charette #1261*, (BRY).

Manitoba: Riding Mountain Park, *G.B. Ownbey #2881*, (CAN); Miniota, *H.J. Scoggan #11199*, (GH); Cowan, *H.J. Scoggan & W.K. Baldwin s.n.*, (GH).

Montana: St. Mary's Lake, Glacier Park, *B. & R. Maguire #15539*, (GH); Westby, *E.L. Larsen #10*, (GH).

Saskatchewan: Saskatoon, *G.W. Argus #9069*, (CAN); McKague, *A.J. Breitung #1218*, (GH).

South Dakota: Nemo, Lawrence Co., *S.L. Welsh #994*, (BRY).

Washington: Okanogan Co., *H. St. John #7703*, (GH).

Wyoming: Laramie Range, Albany Co., *C.L. & M.W. Porter #9824*, (GH); Four Corners, Weston Co., *C.L. Porter #5340*, (GH).

Oxytropis gracilis (A. Nels.) K. Schum. subsp. *dispar* (A. Nels.) Elisens

North Dakota: Glen Ullin, *W.J. Elisens #186*, (ALTA); Belfield, *O.A. Stevens #501*, (GH); Leeds, Benson Co., *S.L. Welsh #878*, (BRY).

Oxytropis cusickii Greenm.

Alberta: Snow Creek Pass, Banff Park, *A.E. Porsild #21424*, (CAN); Mt. Cheviot, Cadomin, *W.J. Elisens #011*, (ALTA); Mt. Carthew, Waterton Park, *W.J. Elisens #130*, (ALTA).
British Columbia: Quiniscoe Lake, Ashnola Range, *J.A. Calder #19599*, (GH).
Montana: Beartooth Mountains, Carbon Co., *A. Cronquist #7988*, (GH); Anaconda-Pintlar Wilderness, Beaverhead Co., *C.L. Hitchcock & C.V. Muhlick #12861*, (RM).
Oregon: Ameroid Lake, Wallowa Mts., Wallowa Co., *A.R. Kruckeberg s.n.*, (RM).
Washington: Mt. Wow, *J.W. Thompson #12578*, (ALTA); Heliotrope Ridge, Mt. Baker, *H. Weitman #10591*, (GH).
Wyoming: Warren Peak, Crook Co., *C.L. & M.W. Porter #10150*, (GH); Medicine Bow Mts., *A. Nelson #9228*, (GH); Boyd, Weston Co., *A. Nelson #9433*, (GH); Gannett Peak, Fremont Co., *F. Jozwik #417*, (GH).

Oxytropis columbiana St. John

Montana: Mud Creek, Glacier Park, *W.J. Elisens #387*, (ALTA); Big Prairie, Glacier Park, *L.H. Harvey #5686*, (MONTU).

Washington: Kettle Falls, Ferry Co., *H.T. Rogers #426*, (GH); Gifford, Stevens Co., *L. Boner & V. Weldert #180*, (GH).

Oxytropis jordalii Porsild subsp. *jordalii*

Alaska: Wiseman, *H.M. Raup & A.J. Soper #9427*, (GH); Juneau, *M.Williams #1397*, (GH); Arctic Village, *L.H. Jordal #3644*, (CAN).

Alberta: Mt. Cheviot, near Cadomin, *W.J. Elisens #224*, (ALTA).

British Columbia: Mt. Mansfield, Haines Rd., *J.Sias #19*, (CAN).

Northwest Territories: Richardson Mts., *S.L. Welsh & J.K. Rigby #12062*, (BRY); MacKenzie Mts., *A.E. Porsild & A.J. Breitung #11817*, (CAN); mile 111E, Canol Rd., *V.C. Wynne-Edwards #8346*, (CAN).

Yukon Territories: mile 81, Dempster Hwy., *R.T. Porsild #1486*, (CAN).

Oxytropis jordalii Porsild subsp.
davisii (Welsh) Elisens

British Columbia: mile 403.5, ALCAN Hwy., *W.J. Elisens #350*, (ALTA); mile 588.5, ALCAN Hwy., *S.L. Welsh & G. Moore #7440*, (BRY); mile 160, ALCAN Hwy., *S.L. Welsh & G. Moore #5431*, (BRY).